Mem. Qd Mus. **17**(2): 195–235, pls. 7–26. [1975]

THE GENUS *MACROPUS* SHAW (MARSUPIALIA: MACROPODIDAE) IN THE UPPER CAINOZOIC DEPOSITS OF QUEENSLAND

ALAN BARTHOLOMAI
Queensland Museum

ABSTRACT

The genus *Macropus* Shaw, 1790, is shown to comprise three subgenera, *M. (Macropus)* Shaw, *M. (Osphranter)* Gould, 1842, and *M. (Prionotemnus)* Stirton, 1955, on the basis of morphological and palaeontological evidence. *M. (Macropus)* is known only from Pleistocene sediments, whereas the other subgenera are also well represented in the late Pliocene Chinchilla Sand. Only two species of *M. (Macropus)* are recorded, the most commonly encountered being *M. titan*, while *M. rama* is described as a new species. Within *M. (Osphranter)*, four species are recognized, *M. altus* and *M. ferragus* from the Pleistocene deposits and *M. pan* and *M. woodsi* sp. nov. from the Chinchilla Sand. *M. (Prionotemnus)* possibly comprises six species, four of which, *M. agilis siva*, *M. gouldi*, *M. piltonensis* sp. nov., and *M. thor*, are restricted to Pleistocene sediments. *M. dryas* and *M. palankarinnicus* are present in the Chinchilla Sand. Palaeontological evidence suggests that *M. (Macropus)* was derived late in the geological history of the group and that within the other subgenera, general and occasionally particular relationships can be suggested for derivation of the recent fauna. Possible phylogenetic relationships within the *M. (Osphranter)* group are suggested back to the late Pliocene. In many species, statistical evaluation of most of the cheek teeth was possible, and comparisons with data from recent macropodids have been made.

Representatives of the genus *Macropus* Shaw are very abundant in the Upper Cainozoic sediments of Queensland. Although some specimens referable to the genus came from widespread localities in Queensland, most have been derived from the Pleistocene fluviatile deposits and the Chinchilla Sand of late Pliocene age, both in the Darling Downs area, southeastern Queensland.

Considerable diversity of opinion has existed regarding the generic limits of the genus *Macropus* and the taxonomy and temporal relationships of referred species. Bartholomai (1967, 1973a*, 1973b) has examined progressively aspects of the overall problem, and the present study clarifies the bulk of the remaining problems. Some of the results of the present study were foreshadowed in Bartholomai, 1972, while preliminary work on part of the older type material was included in a study by Bartholomai (1966). The availability of large samples now enables reassessment of the species to be made, especially aspects of intraspecific variation, utilizing evaluation of the populations by statistical and comparative morphological means. Results contribute to a better overall understanding of the taxonomy of the genus *Macropus*, and suggest that species are of potential value in correlation of Upper Cainozoic continental deposits.

Less detailed investigation has been made of the continental distribution of fossil species of *Macropus*, and until revisionary work has been completed on collections in other Australian museums, conclusions in this area are largely tentative. Exact temporal relationships are frequently difficult to establish away from the type areas.

All measurements are in millimetres.

Genus **Macropus** Shaw, 1790

TYPE SPECIES: *Macropus giganteus* Shaw, 1790 (validated under the plenary powers of the International Commission on Zoological Nomencla-

* Erratum: In Bartholomai (1973a) the illustrations of fossils comprising Plates 21 and 23, but not the captions to these plates, were inadvertently transposed during printing. Thus the caption to Plate 21 refers to the illustrations in Plate 23 and vice versa.

ture, Opinion 760, 1966, by monotypy, as interpreted by the neotype, Queensland Museum specimen, J10749, designated by Calaby *et al.*, 1962, and restated by Calaby and Ride, 1964).

The first large, modern macropodids were collected in 1770, some sixty years before the first fossil representatives of the family were discovered. A party from Captain James Cook's ship, the 'Endeavour' secured three specimens from the vicinity of the Endeavour River, near the present position of Cooktown, and from these Muller (1776) described *Macropus canguru*. The apparent holotype was destroyed during the Second World War through bombing of the Royal College of Surgeons. The identity of the species, however, was in doubt, and Iredale and Troughton (1925) had previously suggested that the specimen described may have been a wallaroo rather than a kangaroo. Further complication was added when these authors (Iredale and Troughton, 1937) suggested that the specimen may have been a Whiptail Wallaby (*Macropus parryi*). Both suggestions were based on unpublished work of Solander (1768–71). Raven (1939) contended that the first description was of a Grey Kangaroo, and this was strongly supported by Morrison-Scott and Sawyer (1950). In an attempt to stabilize the nomenclature, Calaby *et al* (1962) also reaffirmed this position and selected a neotype, Queensland Museum specimen J10749. This specimen is a juvenile Grey Kangaroo collected from the Cooktown area. Ride (1963) commented further on the nomenclatural problem, and this was followed by a revised application by Calaby *et al.* (1963) which resulted in considerable comment. Kirkpatrick (1963) and Woods and Kirkpatrick (1964) indicated that the original specimen was a Wallaroo. Mayr (1964) and Lemche (1964) also commented on details of the case, numbered Z.N.(S.) 1584. New proposals were then outlined by Calaby and Ride (1964), and these were supported by Morrison-Scott (1964) and Finlayson (1964). Another complication was the designation by Troughton and McMichael (1964a, b) of an additional neotype, this being a Whiptail Wallaby. Voting on the case favoured the proposition by Calaby and Ride (1964) and involved the use of the plenary powers, stabilizing the nomenclature under Opinion 760, as indicated above.

Considerable diversity of opinion still remains regarding the generic limits to be applied to the genus *Macropus*, both in terms of its neontological and palaeontological usage. Ride (1962) concluded that 'no confusion would result from the perfectly valid action of any author who writes about a species of wallaby or kangaroo (living or extinct) and prefers to remain non-committal about his generic concepts. Such an author may simply employ *Macropus* . . . or he may follow a stated taxonomic list'.

The problem is not a simple one and the species which may be referred to *Macropus* have been relegated to the following genera (or subgenera) depending on the limits placed by individual taxonomists—*Macropus*, *Halmaturus* (a junior secondary homonym of *Macropus* but used for the purpose of separation), *Osphranter*, *Fissuridon*, *Megaleia*, *Wallabia*, *Thylogale*, *Petrogale*, *Peradorcas*, *Lagorchestes*, *Onychogalea*, *Lagostrophus*, *Dorcopsis*, *Dorcopsulus*, *Dorcopsoides*, *Dendrolagus*, *Setonix*, *Synaptodon*, *Prionotemnus*, *Protemnodon* and *Troposodon*.

Ride (1962) has presented an historical summary of various usages suggested by major contributors to taxonomic interpretation of the group. Genera from the above list which are apparently nomenclaturally stable in recent literature include *Fissuridon*, *Thylogale*, *Petrogale*, *Peradorcas*, *Lagorchestes*, *Onychogalea*, *Lagostrophus*, *Dorcopsis*, *Dorcopsulus*, *Dorcopsoides*, *Dendrolagus*, *Setonix* and *Troposodon*.

Bartholomai (1973a) defined the generic limits of *Protemnodon*, indicating its distinction from other macropodids. Earlier work by Stirton (1963) was supported in the contention that *Protemnodon* is distinct from living kangaroos and wallabies, including the Swamp Wallaby, making available the generic name, *Wallabia*, for at least part of this group.

Progression of the cheek tooth row was considered by De Vis (1895) to be of extreme importance in separation of the Queensland fossil sample into the genera *Halmaturus* and *Macropus*. The process of progression is particularly evident in kangaroos, as shown by Kirkpatrick (1963, 1964) for *M. giganteus*, and later (Kirkpatrick, 1965) restated for this species, and shown for *Megaleia rufa* and *Macropus robustus*, where the extent of the progression has been employed in ageing of specimens. Information on molar progression in *M. rufa* has also been presented in Calaby (1968). Although rate of progression is less pronounced in brush wallabies it is nevertheless significant, as indicated for *M. rufogrisea* by Kirkpatrick (1965), and would appear to represent differences in function in the two groups rather than generic distinction. The degree of movement in *Wallabia bicolor* has not been investigated to the same extent but appears to be generally comparable with that in the brush wallabies.

Cytological investigation of recent macropodines by Sharman (1961) has shown the availab-

ility of characters previously disregarded and this has been followed by Kirsch (1968), who has examined marsupial haemoglobin and has presented preliminary information for many living macropodines. According to details provided by Sharman (1961), chromosome number and sex chromosome morphology indicate the generic distinctness of *Megaleia*, *Setonix* and *Lagostrophus*. In addition, middle-sized wallabies, kangaroos and wallaroos are diphyletic with the type species of *Wallabia*, *W. bicolor*, differing markedly from the rest of this group. Serological studies by Kirsch (1968) suggest that species of wallabies and kangaroos, including *W. bicolor*, *Megaleia* and *Lagorchestes* are closely associated, a conclusion which cannot be verified by the fossil record because of general deficiencies in fossil samples yet available. Sharman *et al.* (1966) have recently investigated reproductive physiology of *W. bicolor*, showing it to be unique among the Macropodidae. Further, Calaby (1966) states that this species differs in behaviour and has distinctive dental characters from the rest of the group. Calaby considers that *Wallabia* should be recognized as a monotypic genus, while the remainder of the wallabies, the Grey Kangaroo and the wallaroos should remain within *Macropus*. This action is supported by the present study.

All members of *Macropus* are characterized by 16 (2N) chromosomes. While differences are evident between species in this grouping, they are nowhere as marked as those enabling separation of *Wallabia*, which has a diploid complement of 10 in the female and 11 in the male. Ride (1970) applies this terminology, but Frith and Calaby (1969) again revert to use of *Macropus* for the Grey Kangaroo and wallaroos and *Wallabia* for all the brush wallabies.

Equal area grid diagrams, as proposed by Thompson (1959), have been shown by Bartholomai (1973a) to be of value in illustrating gross relative size and displacement differences present between skulls of species of *Macropus*, *Wallabia* and *Protemnodon*, based on a skull of *W. bicolor* as a standard. Apart from differences between the genera noted in Bartholomai (1973a), the figures indicate a remarkable uniformity in modification of the grid to *M. giganteus* and the brush wallabies which possess the diploid chromosome number of 16.

Separation of *Macropus* is further supported by the anatomy of the cheek teeth, particularly lower molars. All species referred to *Macropus* have high-crowned lower molars with strong links and with near vertical, lingual lophid margins and non-vertical labial margins. If ornamented, the strongly curved, posterior hypolophid surface is, with rare exception, grooved or pocketed. *Protemnodon* has more rectilinear and generally relatively lower lophids, and has the posterior surface of the hypolophid considerably less curved. Ornamentation of this surface is restricted to development of a posterior cingulum. The permanent premolar is not lost through progression. *Wallabia* has low crowned molars with rectilinear lophids and low links. Lateral margins of the lophids are bulbous, while the posterior hypolophid surface is not ornamented. These characters are of paramount importance in consideration of the fossil material and support the generic distinction of these forms at least. The position of *Synaptodon*, described by De Vis (1889), cannot be resolved at this time, because it is based on inadequate and completely undiagnostic material. The holotype of its type species, *S. aevorum* De Vis, F811, from the late Pliocene Chinchilla Sand at Chinchilla, was stated by De Vis (1895) to be distinguished by peculiar anterior and posterior abutting processes of the molars. Examination has shown that crowns of the molars are almost totally devoid of enamel except for the 'processes' and a small patch on the trigonid basin of the posterior molar. This suggests that the 'processes' may have resulted from weathering, particularly as remaining enamel is soft and chalky, whereas the dentine is hard and mincralized. Certainly no other specimen in the Queensland Museum collections duplicates this condition and no adequate reason apart from abnormal weathering can be suggested for the state of preservation of the holotype.

Megaleia is not represented by fossil material in Queensland. Tedford (1967) records *Megaleia* in the Lake Menindee deposits in western New South Wales but applies the name in the subgeneric sense within *Macropus*. *Megaleia* is distinct from *Macropus* on the basis of modern species but this distinctness becomes diffieult to apply to fossils because of general similarity in cranial morphology between species of both genera. The last molar in the cheek teeth series in *Megaleia* tends to be much larger than that preceding it, a feature not common in species of *Macropus*.

Although the description of the fossil genus *Prionotemnus* Stirton, 1955, is largely inadequate, an investigation of the referred sample in the University of California, Berkeley, indicates that the species is valid and that the name is available for use within the *Macropus* complex.

For the purpose of this study, the genera *Macropus*, *Megaleia*, *Wallabia* and *Protemnodon* are recognized. Within the *Macropus* group, several distinct species groups are apparent and these

are recognizable as far back as the late Pliocene. Broadly speaking, these correspond to the kangaroos (excluding *Megaleia*), the wallaroos and the brush wallabies (excluding *Wallabia*). These groups are regarded as subgenera.

GENERIC DIAGNOSIS: Medium to large macropodines; cranium with rostrum markedly deflected downwards; diastema relatively elongate; lower molars with high lophids, strong links and with lingual margin of lophids near vertical and labial margins markedly divergent; posterior hypolophid surface strongly curved, and where ornamented this comprises a groove, fossette, or very rarely a posterior cingulum.

Subgenus **Macropus** Shaw, 1790

TYPE SPECIES: *Macropus (Macropus) giganteus* Shaw, 1790 (validated under the plenary powers of the International Commission on Zoological Nomenclature, Opinion 760, 1966 by monotypy).

DIAGNOSIS: Medium to large macropodines with palate entire; foramen ovale unhooded and with alisphenoid only slightly grooved at margin of foramen; upper incisors form V-shaped series in occlusal view; I^3 long with labial surface marked by two deep, vertical grooves; basioccipital slightly keeled; postglenoid foramen well-developed; diastema elongate; palate narrow anteriorly; permanent premolars reduced, rapidly lost during progression; upper molars with strong forelink; anterior ridge from paracone usually reduced or absent; infraorbital distance between foramen and anterior rim of orbit short; rostrum not greatly inflated; lower molars with strong posterior groove; mandible broad below anterior cheek teeth.

Subgenus **Osphranter** Gould, 1842

TYPE SPECIES: *Macropus (Osphranter) antilopinus* Gould, 1842 by monotypy.

DIAGNOSIS: Palate entire; foramen ovale hooded, with alisphenoid deeply grooved at margin of foramen; upper incisors form U-shaped series in occlusal view; I^3 quadrangular with labial surface marked by one vertical groove at anterior one-third; basioccipital moderately keeled; postglenoid foramen very reduced; diastema variable but frequently short; palate broad anteriorly; permanent premolars relatively robust, but rapidly lost during progression; upper molars with negligible to weak forelink; anterior ridge from paracone usually reduced but occasionally stronger; infraorbital distance between foramen and anterior rim of orbit long; rostrum moderately to greatly inflated; lower molars with strong posterior groove; mandible excavated and narrow below anterior cheek teeth.

Subgenus **Prionotemnus** Stirton, 1955

TYPE SPECIES: *Macropus (Prionotemnus) palankarinnicus* Stirton, 1955.

DIAGNOSIS: Palate with extensive post-palatine vacuities; foramen ovale hooded, with alisphenoid deeply grooved at margin of foramen; upper incisors form V-shaped series in occlusal view; I^3 triangular with vertical lateral groove in median position or even in posterior moiety; basioccipital markedly keeled; postglenoid foramen well-developed; diastema moderately elongate; palate anteriorly narrow; permanent premolars robust, retained until very old age but occasionally lost through progression; upper molars with minimal forelink; anterior ridge from paracone strong; infraorbital distance between foramen and anterior rim of orbit long; rostrum not greatly inflated; lower molars lacking posterior groove but sometimes with reduced posterior cingulum; mandible broad below anterior cheek teeth.

Macropus (Macropus) titan Owen, 1838

(Plate 7, Figs. 1–2; Plate 8, figs. 1–4; Plate 9, figs. 1–4; Plate 10, figs. 1–3)

Macropus titan Owen, 1838, pp. 359-60, pl. 29, figs. 3-5; 1840-1845, I, p. 392, pl. 101, figs. 1-2; 1845a, p. 236; 1845b, pp. 324-5; 1873, p. 128; 1874a, pp. 248-60, pl. 21, figs. 6-17, pl. 22, figs, 10-8, pl. 23, figs. 2-3, 12-4, pl. 26, figs. 9-15; 1874b, pp. 783-4, pl. 76, figs. 1-6; 1876, pp. 204-9, pl. 25, figs. 1, 4, pl. 26, figs. 1-2; 1877, pp. 400-11, 435-9, pl. 76, figs. 1, 4, pl. 77, figs. 1-2, pl. 78, figs. 1-2, pl. 79, figs. 1-2, pl. 81, figs. 6-17, pl. 82, figs. 10-8, pl. 83, figs. 2-3, 12-14, pl. 86, figs. 9-15; Waterhouse, 1846, pp. 58-9; McCoy, 1862, p. 145; 1867, p. 191; Daintree, 1872, p. 274; Etheridge Jun., 1878, pp. 183-4; 1892, p. 673; Lydekker, 1887, pp. 225-30; Anderson, 1929, pp. 35-9, pl. 17, figs. 1-3, pl. 18, figs. 1-7; Simpson, 1930, p. 73.

Macropus magister De Vis, 1895, pp. 120-4, pl. 18, figs. 11-16; Bartholomai, 1966, pp. 123-4, pl. 19, figs. 1-3.

Macropus faunus De Vis, 1895, pp. 127-9, pl. 18, figs. 3-6; Simpson, 1930, p. 72; Bartholomai, 1966, pp. 122-3, pl. 18, figs. 1-3.

MATERIAL: F3738, cast of holotype, partial right mandibular ramus with M_1 broken, M_2, P_3 removed by fenestration, juvenile, original in British Museum (Natural History), No. 10777, Wellington Caves, N.S.W., from Pleistocene cave deposits (figd Owen, 1838, pl. 29, figs. 3-5; 1874a, pl. 22, figs. 17-8; 1877, pl. 82, figs. 17-18).

F2924, holotype *Macropus faunus* De Vis, partial right maxilla with P^3-M^3, juvenile, Darling Downs (figd in

part, De Vis, 1895, pl. 18, figs. 4-5; figd Bartholomai, 1966, pl. 18, figs. 1-3).

F645, lectotype *Macropus magister* De Vis, partial cranium containing P^2-M^2, P^3 removed by fenestration, juvenile, Ravensthorpe, Pilton, SE.Q., (figd in part, De Vis, 1895, pl. 18, figs. 13-14; figd Bartholomai, 1966, pl. 19, figs.1-3).

Additional material referred to *Macropus titan* Owen comprises 74 juvenile mandibular rami, 126 adult mandibular rami, 4 isolated lower teeth, 11 cranial fragments, 25 juvenile maxillae and 84 adult maxillae from the following localities in the eastern Darling Downs: King Creek; King Creek, at M.R.045455 Clifton 1-mile map; King Creek, at M.R.037455 Clifton 1-mile map; King Creek, near M.R.039454 Clifton 1-mile map; King Creek, near M.R.047452 Clifton 1-mile map; King Creek, Manapouri, at M.R.099465 Liverpool Range 1-mile map; King Creek, at M.R.098465 Liverpool Range 1-mile map; King Creek, at M.R.048457 Clifton 1-mile map; King Creek, between Pilton and Nobby; Ravensthorpe, Pilton; Clifton; ?Pilton; Pilton; Spring Creek; Freestone Creek; Westbrook Creek, near Kingsthorpe; Hirstglen; Gowrie; Gowrie Creek; well at depth of c. 2 m, between Gowrie Creek and radio station 4AK, Oakey; in sewerage drain at c. 10 m, Dalby; near Dalby, Condamine River at Springvale; Jimbour Creek near Dalby; Jimbour Creek, about 3 km south of Jimbour; bank of Condamine River, at M.R.043426 Dalby 1-mile map; Jimbour District; Cambooya, and from the eastern Darling Downs (particular localities unspecified).

A juvenile mandibular ramus from Chinchilla is referred to *M. titan*, as is a juvenile mandible from the Nogoa River, near Rawbelle, mid E.Q., a mandible from Jimboomba, SE.Q., and an adult maxillary fragment from Rubyvale, near Anakie, C.Q.

Specific Diagnosis: A large species. Diastema elongate. P^2 relatively small with longitudinal crest normally bifid and with strong, well-defined posterolingual cuspid, DP_3 and lower molars with high, slightly curved lophids and strong, high links and high anterior cingulum. Posterior surface of hypolophid with near vertical groove and well-defined posterior fossette. P_3 small, usually with bifid longitudinal crest, but occasionally trifid; posterolingual cuspid present, close to posterior cuspid of crest and united to this by high ridge. P^2 with well-defined cusps and high bifid longitudinal crest; protocone least well developed; cuspule present labiad to metacone. DP^3 and upper molars with high lophs and mid-links; forelink present, relatively well-defined. P^3 small, with longitudinal crest normally bifid but occasionally trifid; hypocone well-defined but low; protocone absent.

Description: Mandible moderately deep, relatively thick; base of symphysis deflected at lower level than general base of ramus, near planar; symphysis very elongate, shallow, not ankylosed, rugose; geniohyal pit moderately deep, above posterior symphysial limit; diastema very elongate, with diastemal crest posteriorly acute, less acute anteriorly; ventral margin of ramus rounded between symphysis and extremely weak digastric ridge and process. Mental foramen moderately large, oval, usually set well below diastemal crest, well anterior to anterior root of P_3. Ramus with relatively shallow lateral groove extending posteriorly from just below posterior diastemal crest to below anterior root M_2, close to alveolar margin. Digastric process separated from base of angle by very shallow post-digastric sulcus, bounded above by shallow digastric fossa: this fossa separated above from broad depression opening posteriorly into pterygoid fossa. Post-alveolar shelf short, with angle not well-developed, leading to post-alveolar ridge, ascending posteriorly to disappear on mesial wall of coronoid process, above large mandibular foramen. Masseteric crest raised to about level of occlusion of cheek teeth; masseteric foramen moderately large, with masseteric fossa relatively deep. Angle of mandible markedly inflected. Anterior margin of coronoid process near vertical. Bulk of angle of mandible, coronoid process and condyle not preserved in any specimen.

I_1 elongate, lanceolate, deeply rooted; slightly curved in lateral view, markedly curved in occlusal view, developing subhorizontal facet of wear with upper incisors and mesial wear facet at tip by approximation with other lower incisor; root compressed, oval in section; crown subquadrantal in section, tapering and blade-like anteriorly, enamelled laterally, this produced dorsolabially and ventrolingually into flanges; crown also enamelled ventromesially; distally, subhorizontal dorsal wear facet develops rapidly, but tip is not rounded.

P_2 relatively small, short, approximately suboval in occlusal view, with lingual surface slightly convex and labial surface markedly convex. Anterior cuspid with well defined anterolingual and posterolabial ridges, the latter contributing to a poorly defined longitudinal crest; poorly developed cuspule present along anterolingual ridge; posterolabial cuspid with well-defined anterolingual ridge curving and descending to unite with ridge from anterior cuspid, as continuation of longitudinal crest; crest usually markedly bifid with well defined labial and lingual grooves present near mid-point; occasionally two, well-defined labial grooves are present, in close juxtaposition, corresponding with two lingual grooves, producing a trifid longitudinal crest; grooves sometimes reduced; strong, ornamented lingual ridge occasionally descends from posterior moiety of crest towards posterolingual cuspule; posterior ridge

from posterolabial cuspule curves into mesial posterior groove, sometimes uniting with labial ridge descending from posterolingual cuspule. Major posterior ridge from that cuspule curves anterolingually to terminate in slight basin formed between posterior cuspids; anterior ridge from posterolingual cuspule descends slightly lingually to base of crown towards lingual groove from longitudinal crest. Lingual base of crown sometimes tumescent. Posterior of crown occasionally with angular ridge present at lingual margin.

DP_3 molariform, subrectangular in basal outline, slightly constricted across talonid basin, with lophids moderately high, convex posteriorly. Hypolophid much broader than protolophid. Trigonid basin relatively broad, its length being less than distance between lophids. Forelink high, strong, abruptly curving anterolingually from protoconid to point well labiad to mid-point of high anterior cingulum; cingulum more anteriorly extended at anterolingual margin than elsewhere. Trigonid slopes lingually, and more strongly labially and posteriorly from forelink and cingular margin; well-defined anterolabial fossette present while lingual moiety of trigonid somewhat broadly V-shaped. Slight ridges descend anteriorly and posteriorly from metaconid. Hypoconid with strong, high ridge curving anterolingually across talonid basin as midlink, uniting with strong posterior ridge from protoconid, close to protolophid, labiad to mid-line; weak anterior ridge from entoconid descends into talonid. Talonid slopes labially and lingually from midlink; basin broadly U-shaped in lingual moiety, sharply V-shaped labially; slight accessory ridges occasionally present near anterior of crest of hypolophid. Slight ridge descends posteriorly from entoconid, while stronger ridge descends from near mid-point of posterior surface of hypolophid, curving to posterolingual margin well above crown base, uniting with entoconid ridge to delimit well-defined posterior fossette; fossette emphasised by near vertical, broad groove in posterior surface of hypolophid. Labial bases of lophids much more expansive than lingual, giving crown appearance of flexure about labial limit of talonid; base of crown occasionally slightly tumescent at labial limit of talonid.

P_3 small, short, subtriangular in occlusal view, with crown somewhat constricted at anterior one-third; labial margin slightly convex, while lingual margin markedly concave; anterior cuspid well-defined, usually with moderately weak posterolabial ridge descending as longitudinal crest; anterior ridge poorly defined; posterolabial cuspid also well-defined with anterolingual ridge normally descending to unite with other portion of crest above crown constriction; strong vertical labial and lingual grooves usually present at anterior one-third, giving crest a marked bifid appearance in labial view; grooves sometimes poorly developed with reduction in V-shaped appearance of crest; occasionally second set of vertical labial and lingual grooves present resulting in trifid appearance of crest; normally central area of crest depressed, but occasionally near planar where trifid condition prevails; broad, posterior ridge descends from posterolabial cuspids towards crown base, while high, well-defined lingual ridge unites cuspid with well-defined, but lower posterolingual cuspid; this posterior crest usually concave posteriorly, with broad, vertical, posterior groove present; slight anterior and posterior ridges descend from posterolingual cuspid. Base of crown normally unornamented.

$M_1 < M_2 < M_3 < M_4$; molars subrectangular in basal outline, slightly constricted across talonid basin; lophids high, with hypolophid crest more convex posteriorly than protolophid crest in unworn teeth, similar in worn examples; hypolophid broader than protolophid in M_1, approximately equal in M_2 and M_3, and narrower in M_4. Trigonid basin usually broad; length about equal to distance between lophids. Forelink high, curving anterolingually from protoconid to near mid-point of high anterior cingulum. Cingulum with central portion usually indented and squared in appearance at anterolingual and anterolabial margins; trigonid markedly sloped posteriorly from cingulum, and laterally from forelink; well-defined anterolabial fossette present; labial moiety of trigonid V-shaped, lingual portion sharply U-shaped. Strong, high ridge curves anterolingually from hypoconid across talonid as midlink, uniting with short ridge from labiad to mid-point of protolophid; junction frequently flexed in unworn teeth. Talonid basin decends labially and lingually from midlink; basin V-shaped labially; broadly U-shaped lingually; slight groove occasionally rises from near crown base, near posterolabial margin of base of protolophid; slight ridges usually descend anteriorly and posteriorly from metaconid. Posterior of hypolophid with broad, near vertical groove slightly linguad to mid-line, normally terminating basally in well-defined posterior fossette. Base of crown broadly extended posteriorly, occasionally tumescent at margins of talonid basin. Labial bases of lophids more expansive than lingual, giving crown appearance of flexure about labial margin of talonid.

Cranium known only from partial juvenile specimen and fragmentary supplementary material.

Maxilla laterally with infraorbital foramen opening above anterior margin of P^2 in juvenile cranium, with infra-orbital canal 29·0–40·5 ($\bar{X}$ = 36·1; n = 7) in adult specimens; inferior process of anterior zygoma root moderately strong; palate entire, with palatine well-developed, fenestrated by anterior palatine foramen and posterior lateral foramen; jugal laterally excavated; zygomatic arch markedly sinuous, converging anteriorly; squamosal in narrow anterior contact with frontal, subsquamosal foramen anterodorsal to external auditory meatus, with postzygomatic foramen within meatus opening anteriorly into sinus of root of zygoma; postglenoid process of squamosal moderately well-developed. Ectotympanic deep, complete dorsally, poorly united with squamosal in roof of meatus. Alisphenoid not inflated, in slight contact with basioccipital, with foramen ovale bounded anterolaterally by deep groove. Paraoccipital process elongate.

Upper incisors not known.

P^2 relatively small, subrectangular in basal outline, unknown in unworn condition; crown constricted mesially in occlusal view. Paracone well-defined with strong ridges ascending anteriorly and posteriorly; anterior ridge from metacone ascends to unite with posterior paracone ridge forming bifid longitudinal crest; well-defined, broad vertical labial ridge present below basal constriction. Well-defined posterolabial cuspule present; protocone small, often separated, with slight curving anterolabial ridge developed below crown base; hypocone worn in all examples.

DP^3 molariform, subrectangular in basal outline, slightly constricted across median valley; lophs high, moderately bowed anteriorly; metaloph broader than protoloph. Anterior cingulum moderately high, broad, short, with well-defined forelink linguad to mid-line, from base of protoloph to cingulum; slight anterolingual fossette present; slight ridge ascends anteriorly from paracone often reaching anterolabial limit of cingulum; anterior cingular shelf slopes labially and lingually from forelink. Well-defined, strong, high ridge curves posterolabially from protocone as midlink, uniting with ridge from near mid-point of metaloph, below median valley; weak ridge curves posterolingually from paracone into valley; median valley V-shaped labially and lingually, near planar transversely; lingual moiety often with low fold paralleling floor of valley; broad ridge ascends lingually from hypocone curving anteriorly at crown base, merging with general lingual basal swelling towards margin of median valley. Strong ridge ascends posteriorly from hypocone, curving labially to near posterolabial margin of crown, uniting with slight posterior ridge from metacone; near centre of posterior surface of metaloph, strong groove ascends labially into posterior fossette. Slight grooves present, ornamenting strong ridge from hypocone. Base of crown somewhat swollen.

P^3 moderately small, short, subtriangular in occlusal view, slightly constricted at anterior one-third, usually with well-defined, vertical labial and lingual grooves below constriction, subdividing longitudinal crest. Paracone with well-developed anterior and posterior ridges ascending from cusp; metacone also with ascending, well-defined ridges; anterior ridge from metacone and posterior ridge from paracone comprise longitudinal crest; occasionally two sets of vertical labial and lingual grooves present, giving crest trifid appearance; rarely crest nearly undivided; well-defined ridge connects metacone with lower hypocone; ridges from hypocone curve posterolabially and anteriorly; slight fossette formed well below posterior crown base, behind ridge connecting posterior cusps. Slight indication of basal style occasionally present below metacone.

$M^1 < M^2 < M^3 < M^4$; molars subrectangular in basal outline, slightly constricted across median valley; lophs high, with metaloph crest more convex anteriorly than protoloph crest in unworn teeth, but similar in worn examples; metaloph broader than protoloph in M^1, approximately equal in M^2 and M^3, and narrower in M^4. Anterior cingulum relatively high and broad, moderately short; well-defined, strong forelink ascends from protoloph, well linguad to mid-line, uniting with anterior cingulum near centre of anterior tooth margin; occasionally weak accessory links present paralleling forelink, particularly in labial moiety of anterior cingular shelf; shelf sloped labially and lingually from forelink, and posteriorly from cingulum, sharply U-shaped labially and V-shaped lingually; slight anterior ridge from paracone occasionally unites with labial extremity of cingulum, sharply U-shaped labially and V-present; posterior paracone ridge reduced; base of protoloph often broadly swollen labially, close to midlink. Midlink strong, high, curving posterolabially from protocone to unite with short ridge usually from point on metaloph, linguad to midline; junction often flexed; median valley near planar transversely, only slightly sloping labially and lingually from midlink, V-shaped labially and lingually; Midlink sometimes ornamented labially with accessory ridge to protoloph; low transverse fold in lingual base of valley sometimes present; slight ridges ascend anteriorly and posteriorly from metacone; strong, slightly flared ridge ascends posterolabially from hypocone to posterolabial

TABLE 1: SUMMARY OF MEASUREMENTS FOR *Macropus(Macropus) titan* OWEN

Character	Maxillae					Mandibles				
	n	O.R.	$\bar{X}$	s	V	n	O.R.	$\bar{X}$	s	V
P^2_2 length	6	9·2– 9·8	9·5	0·249	2·62	20	7·3– 9·0	8·3	0·467	5·62
max. width	5	6·6– 7·3	6·9	0·308	4·47	19	3·6– 4·9	4·5	0·283	6·29
DP^3_3 length	12	10·1–11·8	10·9	0·508	4·66	39	10·3–11·8	11·0	0·426	3·88
prot. width	9	7·9– 9·3	8·4	0·534	6·36		5·5– 6·6	6·0	0·260	4·33
P^3_3 length	20	8·5–11·6	9·9	0·741	7·48	30	6·3– 9·2	7·4	0·577	7·80
max. width	17	4·8– 6·3	5·4	0·417	7·72	25	3·5– 5·0	4·0	0·325	8·13
M^1_1 length	46	10·6–14·7	12·3	0·936	7·61	56	11·6–14·1	13·0	0·604	4·65
prot. width	32	8·2–10·7	9·7	0·644	6·64	47	6·9– 8·7	7·6	0·342	4·50
M^2_2 length	77	12·4–16·7	13·9	0·869	6·25	59	12·9–17·0	14·5	0·888	6·13
prot. width	54	9·4–12·8	11·1	0·730	6·58	49	8·1–10·1	9·0	0·421	4·68
M^3_3 length	88	13·7–18·3	15·4	0·827	5·37	111	13·3–18·3	16·5	0·912	5·60
prot. width	70	10·3–14·8	12·4	0·780	6·29	102	8·3–11·0	9·7	0·550	5·67
M^4_4 length	69	14·8–18·9	16·6	0·742	4·47	109	15·5–19·6	17·5	0·941	5·38
prot. width	69	11·4–14·6	12·9	0·724	5·61	103	8·3–11·5	10·3	0·614	5·96

prot. = protoloph or protolophid.

margin below crown base, with production of posterior fossette; broad, near vertical groove in surface of metaloph often contributes to define this; sharp vertical groove frequently ornaments strong hypocone ridge linguad to mid-line. Base of crown often swollen, particularly at lingual extremity of median valley.

DISCUSSION: The partial right mandibular ramus which constitutes the holotype of *Macropus titan* Owen, was among the first marsupial fossils described from Australia (Owen, 1838), having been discovered by Major Sir T. L. Mitchell in cave deposits in the Wellington Valley, New South Wales and forwarded to England for determination by Sir Richard Owen. Although presenting few morphological characters apart from the unworn permanent premolar, later removed by fenestration, this tooth is sufficiently diagnostic to allow reference of subsequently obtained material. Similarity of the specimen to the living kangaroo, *M. major* was noted by Owen (1838, p. 359), but comparison was restricted to size only.

In later publications, Owen (1845b, 1874a) referred mandibular specimens from the Darling Downs to *M. titan*, and correctly assigned and described the upper dentition. Later, Owen (1876) described and figured a well-preserved cranium from King Creek.

McCoy (1879) and Lydekker (1887) considered *M. titan* Owen to be closely allied to *M. giganteus*, being distinguished only by its superior size and the occurrence of a groove or grooves on the posterior surface of the hypolophid. Lydekker indicated the probability that the two forms may pass imperceptibly into one another. No distinction was drawn between the sample from the Darling Downs and that from the type locality.

On the other hand, De Vis (1895) separated the Queensland material, describing *M. magister* and *M. faunus*, from the Pleistocene fluviatile deposits. Justification for naming *M. magister* was expressed in terms of supposed differences in proportions of M_2 between Queensland specimens and the holotype, the supposed lack of a groove in the posterior hypolophid surface of M_2 in *M. titan*, and minor differences in the structure of the trigonid basin and anterior cingulum. De Vis (1895) completely neglected the permanent premolar in his comparison, and gave no indication of knowing of the presence of such a tooth in the holotype, considering the holotype to present only 'a single perfect tooth, M_2'. This tooth, in fact, is fractured posteriorly and lacks the posterior hypolophid surface. *M. faunus* was separated largely because of the tricuspid crest of the upper and lower premolars. This feature is clearly derived from the normal bifid crest in *M. titan*, being achieved through observed intermediate stages in the large sample currently available.

Anderson (1929) considered the separation of the Queensland sample of *M. magister* from *M. titan* and concluded that there were no valid grounds for De Vis' (1895) suggestion, and relegated *M. magister* to synonymy. Anderson proposed that it is unlikely that *M. titan* and *M. giganteus* grade into one another, or that *M. giganteus* is a direct descendant of *M. titan*, but presented only the evidence of slightly more complex molars in the fossil material to support this.

Tedford (1967), gives statistical data for *M. titan* from Wellington Caves in the collections of the Australian Museum, Sydney, and presents population parameters for some tooth dimensions of fossil and living samples of species of *Macropus*. He

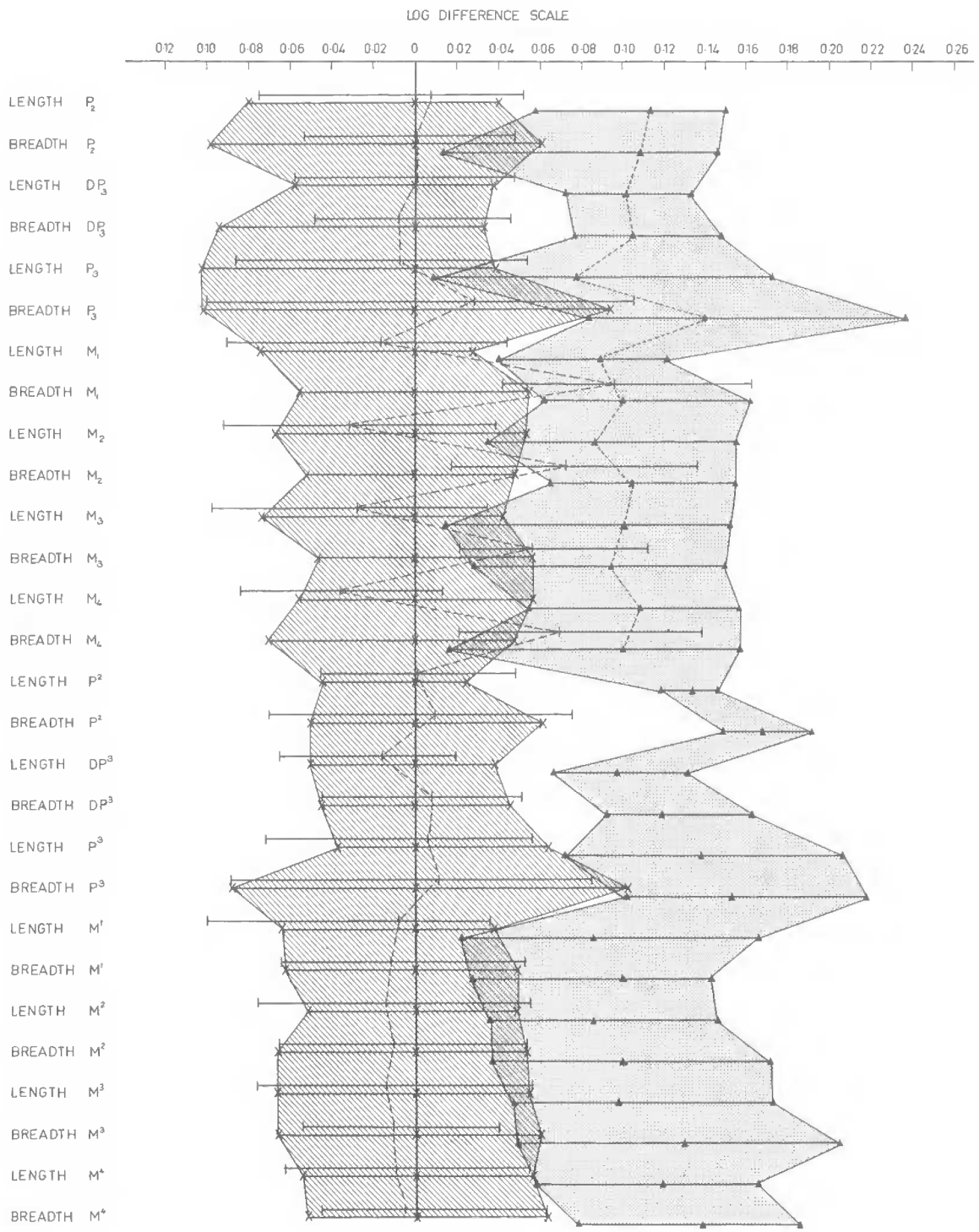


FIG. 1: Log Difference Diagram showing proportional relationships of cheek-teeth in *Macropus (Macropus) titan* (stippled) using mean values in the Queensland sample of *M. giganteus* (cross hatched) as standard. Data for Warwick sample of *M. giganteus* overlain.

TABLE 2: SUMMARY OF MEASUREMENTS FOR *Macropus (Macropus) giganteus* SHAW (QUEENSLAND SAMPLE)

Character	Maxillae					Mandibles				
	n	O.R.	$\bar{X}$	s	V	n	O.R.	$\bar{X}$	s	V
P^2_2 length	35	6·3– 7·7	7·0	0·326	4·63	34	5·3– 7·0	6·4	0·339	5·32
max. width P^2_2	28	4·2– 5·4	4·7	0·249	5·28	34	2·8– 4·0	3·5	0·285	8·27
DP^3_3 length	45	7·8– 9·5	8·7	0·468	5·39	42	7·8– 9·5	8·7	0·398	4·60
prot. width	43	5·8– 7·1	6·4	0·345	5·43	41	3·8– 5·2	4·7	0·277	5·89
P^3_3 length	25	6·6– 8·3	7·2	0·407	5·63	20	4·9– 7·1	6·2	0·608	9·87
prot. width	25	3·1– 4·8	3·8	0·390	10·31	20	2·3– 3·6	2·9	0·323	11·19
M^1_1 length	77	8·7–11·0	10·1	0·469	4·66	66	8·9–11·3	10·6	0·630	5·97
prot. width	75	6·7– 8·6	7·7	0·411	5·35	60	5·4– 6·8	6·0	0·293	4·86
M^2_2 length	80	10·2–12·8	11·5	0·587	5·10	71	10·2–13·5	11·9	0·674	5·65
prot. width	78	7·4– 9·7	8·6	0·482	5·59	71	6·3– 7·9	7·1	0·345	4·86
M^3_3 length	61	10·6–14·0	12·3	0·711	5·79	50	10·9–14·2	12·9	0·675	5·26
Prot. width	58	7·9–10·7	9·2	0·558	6·06	48	7·0– 8·7	7·8	0·461	5·95
M^4_4 length	37	11·4–14·7	12·9	0·776	6·03	34	12·2–15·2	13·6	0·828	6·10
prot. width	34	8·5–11·0	9·5	0·613	6·47	34	6·8– 8·9	8·0	0·484	6·04

prot. = protoloph or protolophid.

also illustrates a log difference diagram comparing the juvenile cranium of *M. titan* described and figured by Anderson (1929) and previously figured by Ramsay (1882), with crania of recent species. Marked differences in proportions are indicated but, as suggested by Tedford (1967), some of the discrepancies may result from slight differences in maturity of the examples plotted. In juvenile specimens, such age differences could, in fact, result in marked proportional differences and the result of the comparison may not be entirely valid.

Certainly in other parameters, such as dimensions of cheek teeth, no outstanding discrepancies exist, particularly where the plotted values are derived from reasonably large living and fossil populations. In detail, however, different samples of the same species show some divergence.

The log difference diagram given here (Fig. 1) compares the relative proportions of the cheek teeth in *M. titan* with the standard provided by the mean values for Queensland *M. giganteus* (Table 2), and includes separate data for a geographically restricted sample of that species from the Warwick district, southeastern Queensland, published by Bartholomai (1971). Shading in the log difference diagram provides visual separation of comparisons of observed values for characters in two of the samples, and indicates those parameters where overlap occurs. Area have no signficance. Presenting the diagram in this form reduces confusion resulting from incorporation of data from the number of samples considered. The diagram illustrates general overlap of the samples of *M. giganteus*, but shows the relatively broader nature of the lower molars in the Warwick sample, compared with the Queensland sample. On a proportional basis, *M. titan* compares better with this latter material than with that from Warwick. This unexpected deviation within samples of the same species suggests that even with large samples of *Macropus* only generalised conclusions can be drawn from log difference diagrams.

M. birdselli, described by Tedford (1967), is very similar to *M. titan* in all of the characters presented, with the exception of the length of the diastema. In *M. titan*, Table 3 presents measurements for the length of the lower diastema, indicating that no overlap occurs with the *M. birdselli* sample. Dimensions of cheek teeth in *M. birdselli*, presented in Tedford (1967), fall well within the range of observed values for *M. titan*. Tedford (1967) has suggested a relationship between *M. birdselli* and *M. fuliginosus*, the Kangaroo Island and western mainland Grey Kangaroo and, on the basis of diastemal length and other morphological details, this is considered here to be a strong possibility. *M. birdselli* is maintained although, in most morphological features, considerable similarity exists with *M. titan*. Larger samples of *M. birdselli* will be required to ascertain whether variants of such features as diastemal length overlap with those in *M. titan*.

TABLE 3: LENGTH OF LOWER DIASTEMA IN *Macropus titan* OWEN

Specimen	F4198	F646	F4145	F3722	F4171	F4186
Diastema length	60·7	59·5	61·0	53·8	52·1	64·3

Summaries of measurements for lower and upper cheek teeth in *M. titan* are presented in Table

1. The size of the fossil samples is adequate for most characters considered. Only the deciduous upper dentition is poorly represented. As suggested by the Coefficient of Variation, the sample is likely to be homogeneous, and is in keeping with values for V provided from the Queensland and Warwick samples of *M. giganteus*. The generally high values for V associated with the permanent premolars indicate that the fossil sample in this case is somewhat less variable than *M. giganteus*.

Structurally, *M. titan* is very similar to *M. giganteus*, the most obvious difference being that of size. Grooving on the posterior surface of the hypolophid is less well-developed in *M. giganteus*, and the posterior fossette, usually present in *M. titan*, is normally absent in the recent species. In other features of the dentition and cranial morphology presented in the Queensland sample, no marked differences occur. Results of a statistical comparison of the fossil sample with the Warwick sample of *M. giganteus* are presented in Table 4 and show that whereas breadths of lower teeth are generally broader than in the Queensland sample, only the breadth of M_1 does not appear significantly different from that in *M. titan*. Using Students–t test, all other characters give probability values of 0·001. The Coefficient of Difference is generally larger than the 1·5 value considered by Ride (1964) as sufficient for the recognition of subspecific distinctness, usually being less than this only with respect to breadths of lower molar teeth. Comparison with the Queensland sample would provide much higher values for C.D. for breadths of lower molars, because of lower values for $\overline{X}$ in that sample.

Because of the morphological differences noted, it is felt that the fossil sample is sufficiently distinct from the recent material to justify its separation at the specific level. Close relationship with the recent *M. giganteus* appears highly likely. No attempt has been made to associate post-cranial remains with the referred cranial remains.

In the Darling Downs, apart from one mandibular specimen, F4230, *M. titan* is currently restricted to the Pleistocene fluviatile deposits of the eastern Darling Downs. F4230 was collected from Chinchilla, but its preservation is not indicative of derivation from the Chinchilla Sand. It may have been recovered from one of the presumably younger terraces, possibly of Pleistocene age, which are associated with the Condamine River and Charley Creek, in the Chinchilla area. Lack of material referable to *M. titan* in the extensive collections from the Chinchilla Sand would support this suggestion. Other Queensland localities for the species are indicated in the list of material referred. Although probably widespread in eastern Australia, such occurrences as that indicated by Glauert (1912) from Western Australia, need to be checked against *M. birdselli* and *M. fuliginosus* before any synthesis is made of the Australian distribution for the species.

Macropus (Macropus) rama sp. nov.
(Plate 11, figs. 1–4)

MATERIAL: F4773, associated left mandibular ramus with P_3–M_4, and right maxilla with P^3–M^3, adult, bend in King Creek, Pilton, at M.R.134444 Liverpool Range 1-mile map, eastern Darling Downs, SE.Q., in Pleistocene fluviatile deposits.

TABLE 4: COMPARISON OF THE WARWICK SAMPLE OF *M. giganteus* WITH THAT FOR *M. titan*

	Maxillae			Mandibles		
Character	t	P	C.D.	t	P	C.D.
P^2_2 length	20·7142	0·001	4·65	19·4400	0·001	2·20
max. width	15·1364	0·001	3·47	7·4582	0·001	2·09
DP^3_3 length	19·0282	0·001	2·70	28·4010	0·001	3·01
prot. width	14·7660	0·001	2·30	26·5232	0·001	2·91
P^3_3 length	16·3836	0·001	2·10	10·4586	0·001	1·25
max. width	13·7666	0·001	1·93	10·3157	0·001	1·33
M^1_1 length	21·2534	0·001	1·63	29·7851	0·001	2·45
prot. width	23·5865	0·001	2·06	1·4543	0·2–0·1	0·13
M^2_2 length	26·3636	0·001	1·84	9·2853	0·001	2·20
prot. width	30·4934	0·001	2·29	8·0134	0·001	0·68
M^3_3 length	32·1624	0·001	2·41	37·2105	0·001	2·72
prot. width	34·0161	0·001	2·68	13·3205	0·001	0·77
M^4_4 length	32·9439	0·001	2·96	36·7419	0·001	3·22
Prot. width	30·5746	0·001	2·79	9·3852	0·001	0·78

prot. = protoloph or protolophid.

SPECIFIC DIAGNOSIS: Relatively small species. Lower molars with trigonid basin widely spatulate in form and with hollowing of the posterior base of protolophid; lateral surfaces of lophids very narrow; hypolophid grooved at posterolingual base of crown. Upper molars lacking well-defined forelink.

DESCRIPTION: I_1, P_2 and DP_3 unknown.

Mandible moderately shallow, robust and with moderately long post-alveolar shelf, but too incomplete for further description.

P_3 small, suboval in basal outline, being slightly constricted mesially. Longitudinal crest bifid, with well-defined anterior and posterior cuspids, separated mesially by prominent vertical labial and lingual grooves; posterior extension of crest descending directly to base of crown; lingual and anterior bases of crown slightly swollen.

$M_1 < M_2 < M_3 < M_4$; molars subrectangular in basal outline, considerably constricted across talonid basin; lophids moderately low, with protolophid broader than hypolophid in M_1 and M_2 and narrower in M_3 and M_4; hypolophid somewhat convex posteriorly, but protolophid nearly rectilinear and showing concave posterior surface in M_3 and M_4; lingual surfaces very narrow basally but with labial surfaces somewhat broader. Lateral surfaces of lophids moderately convex from base to crest. Trigonid basin extremely broad, spatulate, with moderately high, very broad anterior cingulum; length of trigonid approximates distance between lophids. Forelink moderately high, strong, curving anterolingually from protoconid to near mid-point of anterior cingulum. Trigonid gently descends ventrally in both labial and lingual moieties. Accessory link occasionally present near forelink, across lingual moiety of trigonid; slight fossette variably present near base of protolophid, at labial extremity of trigonid. Posterior surface of protolophid variably ornamented with a slight vertical ridge linguad to midlink. Midlink strong, moderately high, curving anterolingually from hypoconid to unite with extremely slight ridge from near mid-point of protolophid. Talonid basin V-shaped in labial and lingual moieties. Posterior surface of hypolophid broadly rounded, marked by relatively strong vertical groove towards posterolingual base of crown, and by variable, slight vertical grooves mesially.

I^{1-3}, P^2, DP^3 and M^4 unknown.

P^3 moderately small, subovate in basal outline, being much broader posteriorly than anteriorly. Longitudinal crest subdivided mesially by well-defined vertical labial and lingual grooves giving crest a bifid appearance; anterior moiety transected by a pair of weak vertical labial and lingual ridges, with production of cuspule at crest; posterior extension of crest ascending directly towards base of crown; crown worn posterolingually, but remaining ridges suggest presence of posterolingual cusp. Labial and anterior bases of crown slightly swollen.

$M^1 < M^2 < M^3$; molars subrectangular in basal outline, considerably constricted across median valley; lophs relatively low, moderately convex anteriorly, but apparently less so across protoloph; protoloph narrower than metaloph in M^1 and broader in M^2 and M^3. Anterior cingulum moderately low, short, very broad ascending labially and lingually from axis of crown, worn mesially, with no trace remaining of forelink. Midlink moderately high, strong curving posterolabially from protocone to unite with short ridge from near mid-point of metaloph. Median valley V-shaped; posterolabial base of protoloph variably marked by transverse groove. Strong ridge ascends from hypocone towards base of crown, uniting posterolabially with posterior of metaloph with production of posterior fossette; slight, variable ridges ascend into fossette from metaloph.

DISCUSSION: The present material represents one of the few instances in the Pleistocene fluviatile deposits of the eastern Darling Downs of associated mandibular and cranial specimens. Although from different sides of the skull, the specimens were located together, and show morphological compatibility, similar stages of dental eruption, complementary wear patterns and similar size. Also located in the same isolated pocket of fossils were a partial right pelvis containing the acetabulum and remnants of the ilium, ischium and pubis, and the distal end of a left humerus. While it is possible that these macropodid post-cranial remains also belong to the same individual from which the skull remains were derived, no supplementary evidence can be presented to prove their association. Compared with modern macropodids, their size is in keeping with the size of the skull remains referred to *M. rama*.

The cranial remains show some morphological similarity to *M. giganteus* Shaw, but are considered to be specifically distinct. The permanent upper and lower premolars are similar to those in *M. giganteus*. P_3 shows no posterior incurving of the longitudinal crest, a feature observed rarely in *M. giganteus*. In *M. rama* the trigonid basin is widely spatulate in form, whereas that in *M. giganteus* is usually considerably narrower. Extreme variants of the modern species show some tendency towards broadening of the trigonid. The hollowing of the posterior base of the protolophid is seen in many

TABLE 5: MEASUREMENTS FOR *Macropus (Macropus) rama* SP. NOV.

Specimen	P_3	M_1	M_2	M_3	M_4	P^3	M^1	M^2	M^3
F4773	5·2 × 2·7	7·7 × 4·7	9·7 × 6·7	10·7 × 8·2	12·2 × 8·7	7·6 × 4·0	9·0 × —	9·9 × 8·1	11·2 × 8·7

examples in *M. giganteus*, but the narrowness of the lateral surfaces of the lophids is not duplicated to the same degree. The position of the posterior vertical groove at the posterolingual base of the crown is not usual for *M. giganteus*. In the upper molars, no trace remains of the presence of a forelink, a feature present in *M. giganteus*. The teeth are all well worn and traces of a forelink are frequently obliterated in similarly worn teeth in the modern species. Other differences in upper molars are within the range of variation for *M. giganteus*.

As can be seen from Table 5, the size of the fossil form is smaller than generally seen in *M. giganteus*, even in females of that species (Bartholomai, 1971), and is considerably smaller than *M. titan* (Table 1), the most commonly encountered species of *Macropus* in the Pleistocene fluviatile deposits of the Darling Downs.

Macropus (Osphranter) altus (Owen, 1874)
(Plate 12, figs. 1–2; Plate 13, figs. 1–2; Plate 26, figs. 3–4)

?*Macropus titan* Owen, 1838, p. 360, pl. 29, figs. 4–5.
Osphranter cooperi Owen, 1874, p. 261, pl. 24, figs. 17–18.
Phascolargus altus Owen, 1874, pp. 261–4, pl. 22, figs. 1–2; 1877, pp. 413–6, pl. 82, figs. 1–2, pl. 111, ?figs. 1–6, pl. 117, ?figs. 1–6; Etheridge Jun., 1878, p. 187; 1892, p. 676.
?*Phascolargus altus* Owen, 1876, p. 218, pl. 30, figs. 1–5.
Macropus (Osphranter) cooperi (Owen): Owen, 1877, pp. 412-3, pl. 84, figs. 17–18.
Macropus altus (Owen): Lydekker, 1887, pp. 223–4; Simpson, 1930, p. 71.
Macropus cooperi (Owen): Lydekker, 1887, p. 224; Simpson, 1930, p. 71.
Halmaturus cooperi (owen): De Vis, 1895 *partim*, pp. 116–8, pl. 17, figs. 24–7.

MATERIAL: F3399, cast of holotype of *Phascolargus altus* (Owen), British Museum (Natural History) specimen, juvenile palate with left P^2–M^2, M^3 exposed laterally, right DP^3–M^2, P^3 and M^3 exposed laterally, cave in Wellington Valley, New South Wales, from Pleistocene cave earth deposits (figd Owen, 1838, pl. 29, figs. 4–5; 1874, pl. 22, figs. 1–2; 1877, pl. 82, figs. 1–2).

F2849, juvenile right maxilla with P^3 exposed by fenestration, M^1–M^3, Bongeen, Darling Downs.

F5608, cast of holotype *Osphranter cooperi* Owen, British Museum (Natural History) specimen number 32886, partial left mandibular ramus with I_1, broken, P_3–M_2, adult, Condamine River, Queensland, (figd Owen, 1874, pl. 24, figs. 17–8; 1877, pl. 84, figs. 17–8).

F5441, partial right mandibular ramus with M_2–M_4, eastern Darling Downs.

SPECIFIC DIAGNOSIS: Comparatively large species; P^3 well-developed, moderately elongate with longitudinal crest straight, transected by two sets of ridges between paracone and metacone; hypocone low, with anterolabial ridge connecting to above metacone; lingual cingulum low, extending to above paracone; labial and anterior base of crown swollen. Upper molars with moderately high lophs; anterior cingulum low, slightly recurved, and with variable forelink, rarely strong; ridge from paracone usually links with labial limit of cingulum. P_3 relatively elongate with trifid longitudinal crest. Lower molars with moderately high lophids, links and anterior cingulum; posterior surface of hypolophid with deep, near vertical groove, flanked by slightly flared margins.

DESCRIPTION: Cranium known only from fragmentary palate and maxillary specimens. Palate entire.

I^{1-3} and M^4 unknown.

P^2 moderately elongate, subovate in occlusal view, with longitudinal crest between paracone and metacone slightly concave labially, low; crest transected by two sets of vertical labial and lingual ridges with indication of cuspules on crest. Lingual cingulum low, but posterolingual portion of crown worn; cingulum extends anterolingual to paracone.

TABLE 6: MEASUREMENTS FOR *Macropus (Osphranter) altus* (OWEN) MAXILLA

Specimen	P^2	DP^3	P^3	M^1	M^2	M^3
F3399, right*	9·1 × 5·1	9·8 × 7·0	—	11·1 × 9·4	12·9 × 10·0	—
F3399, left	—	—	10·0 × —	11·4 × 9·2	13·3 × 10·5	15·3 × —
F2849	—	—	9·8 × 5·0	10·7 × —	12·6 × —	— × 10·0

*Holotype *M. altus* (Owen)

DP^3 molariform, subtriangular in occlusal view, very slightly constricted across median valley; lophs moderately high, anteriorly convex with protoloph much narrower than metaloph. Anterior cingulum low, broad, with anterior cingular shelf moderately short; weak forelink present, uniting cingulum with protoloph base, linguad to mid-line; ridge from paracone connects with labial limit of cingulum. Midlink strong, high, curving posterolabially than lingually, nearly planar transversely. from near mid-point of metaloph above median valley; median valley more sharply U-shaped labially than lingually, near - planar transversely. Posterior ridge from metacone weak, ascending slightly lingually to unite with much stronger ridge from hypocone which curves posterolabially to margin of crown; posterior surface of metaloph excavated below ridges.

P^3 relatively elongate and low-crowned, subovate in occlusal view with longitudinal crest between paracone and metacone straight, low; crest transected by two sets of vertical labial and lingual ridges with production of cuspules on crest. Paracone well-defined. Hypocone low, posterolingual to metacone; posterior ridge from hypocone curves labially to unite with posterolingually curving ridge from metacone; very shallow posterior fossette developed between these and anterolabial ridge connecting hypocone to above metacone. Anterior ridge from hypocone ascends sharply towards crown base, continuing anteriorly as low, swollen lingual cingulum to above paracone; lingual basin shallow, narrow. Labial and anterior base of crown swollen, delimited from rest of crown by well-defined groove.

$M^1 < M^2 < M^3$; molars subrectangular in occlusal view with moderately high lophs; lophs convex anteriorly. Protoloph slightly narrower than metaloph in M^1 and M^2 and approximately equal in M^3. Anterior cingulum low, broad, with anterior cingular shelf relatively short; cingulum slightly recurved, usually connected to mesial base of protoloph by variable, occasionally strong, forelink; shelf ascends slightly away from forelink; anterior ridge from paracone often well-defined, connecting with labial limit of anterior cingulum; posterior ridge from paracone weak. Midlink strong, high, ascending from protocone across median valley to unite with slight ridge from near mid-point of metaloph; midlink lunate in unworn teeth; median valley sharply U-shaped, tending to be more V-shaped lingually, near planar transversely. Posterior ridge from metacone weak, ascending slightly lingually to unite with much stronger, slightly flared ridge curving posterolabially from hypocone; ridge from hypocone occasionally ornamented by slight accessory ridges; posterior surface of metaloph broadly excavated above junction, with production of posterior fossette.

Mandible known only from fragmentary rami; ramus moderately deep anteriorly, relatively broad, but markedly excavated laterally near alveolar margin below anterior cheek teeth and posterior of diastema; diastemal crest acute posteriorly. Symphysis rugose, not ankylosed, somewhat ventrally deflected, with geniohyal pit deep, positioned at posterior symphysial limit. Ventral margin of ramus behind symphysis rounded, with digastric ridge and process very poorly developed, separated from base of angle by extremely weak post-digastric sulcus; process separated above by fossa with broad, shallow groove extending posteriorly into pterygoid fossa. Post-alveolar shelf short with shelf angle not developed, leading to post-alveolar ridge which ascends onto coronoid process, disappearing above large mandibular foramen; anterior wall of process near vertical, but angle of mandible, bulk of process and condyle not preserved.

I_1, P_2, DP_3 and M_1 are not known as yet.

P_3 relatively elongate, subovate in basal outline; longitudinal crest markedly trifid, with mesial cuspule as well-developed as posterior cuspid and better developed than anterior cuspid. Labial base of crown swollen, delimited from remainder of crown by slight longitudinal groove.

$M_2 < M_3 < M_4$; molars subrectangular in occlusal view, slightly constricted across talonid basin, with lophids relatively high, convex posteriorly; hypolophid much narrower than protolophid in M_4; anterior cingulum moderately high, broad, more expansive anterolingually than anterolabially, marked by vertical furrow slightly labiad to mid-line; forelink descends from protoconid, curving anterolingually across trigonid

TABLE 7: MEASUREMENTS FOR *Macropus (Osphranter) altus* (OWEN), MANDIBLE

Specimen	P_3	M_1	M_2	M_3	M_4
F5608*	6·7 × 3·0	—	—	—	—
F5441	—	—	13·2 × —	15·3 × —	17·4 × 9·0

*Holotype *M. cooperi* (Owen)

basin to unite with cingulum labiad to mid-line. Trigonid basin elongate, about as long as distance between lophids, sloping labially and lingually from forelink as well as posteriorly from cingulum; very slight anterolabial fossette present; slight ridges descend anteriorly and posteriorly from metaconid. Midlink strong, high, descending labiad to mid-line, anterolingually from hypoconid across talonid basin to unite with slight ridge from near protoconid; junction frequently flexed; talonid broadly U-shaped lingually, V-shaped labially, near planar tranversely, sometimes with low transverse fold in floor of lingual moiety. Posterior hypolophid surface with deep, near vertical groove developed linguad to mid-line, bounded laterally by slight ridges. Labial lophid bases more expansive than lingual, with slight groove usually present near posterolabial margin of protolophid.

Discussion: The holotype of *Phascolargus altus* Owen, 1874, was among material forwarded to Owen, following its collection by Major Sir Thomas Mitchell from caves in the Wellington Valley, New South Wales. It represents one of the first known fossil macropodid specimens. When figured by Owen (1838) it was doubtfully referred to *M. titan* Owen but its distinctness from that species was later confirmed (Owen, 1874) when it was described as *Phascolargus altus*. Lydekker (1887) relegated the genus *Phascolargus* to synonymy with *Macropus*, while both Iredale and Troughton (1934) and Tate (1948) indicated the belief that *Phascolargus* represented a junior synonym of *Osphranter*. This conclusion is here maintained on the basis of its cranial and dental morphology.

In addition to his description of *P. altus*, Owen (1874) defined *O. cooperi*. It was unfortunate that Owen chose to base this latter species on such inadequate, poorly preserved material. Uncertainty about the morphology of *O. cooperi* has led subsequent workers, particularly Lydekker (1887) and De Vis (1895), into error in interpretation of the limits and affinities of *O. cooperi*. It is likely that not one of the specimens referred by De Vis (1895) was *M. cooperi*. Not only is the permanent lower premolar the only tooth in the holotype sufficiently well preserved to be described, but also the mandible is not well preserved. This has led to incorrect assumptions regarding the diastemal slope (Lydekker, 1887). The specimen has been fractured and movement has occurred along an oblique line immediately anterior to P_3, effectively reducing the anterior depth of the ramus and the diastemal slope. In addition, the specimen has suffered some lateral crushing.

Maxillary and mandibular remains in *M. altus* have not, as yet, been located associated and synonymy of the mandibular remains of *O. cooperi* with the maxillary remains of *M. altus* has been undertaken on the basis of morphological compatibility and size.

The better preserved holotype of *M. altus* presents many features which enable reference of additional material to the taxon. Although the name *O. cooperi* has page priority over *M. altus* and has been more widely applied subsequently, Owen's application of the names has not been questioned. It is here considered that taxonomy can be better served by recognition of *O. cooperi* as a junior synonym of *M. altus*.

The dentition in *M. altus* is similar to that in *M. ferragus*, described below, and this supports the present association. *M. altus* differs from *M. ferragus* not only in its smaller size but also in the comparatively lower crown heights of its molars, the more longitudinal arrangement of the cuspids and cuspule of the longitudinal crest in P_3, the generally stronger forelink in upper molars, the weaker posterolingual fossette in P^3 and the lack of an anterolingual extension of the lingual cingulum in that tooth.

Compared with living species, *M. altus* differs in being somewhat larger than *M. robustus* and *M. antilopinus*, but because of the small size of the fossil sample, no statistical evaluation and comparison of samples has been possible. P^3 in *M. altus* is more robust, being more strongly developed in its lingual cingulum than the living species. Forelinks in upper molars are generally stronger than in *M. robustus* and are similar to those in *M. antilopinus*. Both *M. robustus* and *M. antilopinus* have well-developed posterolingual cuspids on P^3. Morphological variation is all but unknown in *M. altus* and this could account for some of the differences noted.

The status of the post-cranial material referred to the species by Owen (1877) is extremely doubtful. Until more complete, associated specimens are located, the identity of these specimens cannot be determined.

Eleven specimens in the collections of the British Museum (Natural History) were referred to *M. altus* by Lydekker (1887) and were listed as being derived from the Wellington Caves and Kerban, near Mendoran in New South Wales and from Eton Vale, Gowrie, and the Condamine River in Queensland. The status of these specimens is unknown. While additional specimens are present

in the collections of the Australian Museum, Sydney, which may be referred to *M. altus*, the species is one of the poorest represented in the Pleistocene deposits of the eastern Darling Downs. It is unknown from older sediments.

Macropus (Osphranter) ferragus Owen, 1874
(Plate 14, figs. 1–2; Plate 15, figs. 1–2)

Macropus ferragus Owen, 1874, p. 784, pl. 81, fig. 4, pl. 82, figs. 3–4, pl. 83, fig. 3; Lydekker, 1887, pp. 230–1; Simpson, 1930 p. 72.
Macropus (Leptosiagon) gracilis Owen, 1874, pp. 785–6, pl. 76, figs. 11–15; 1877, pp. 450–1, pl. 89, figs. 11–15.
Macropus (Pachysiagon) ferragus Owen, 1877, pp. 449–50, pl. 91, fig. 4, pl. 92, figs. 3–4, pl. 93, fig. 3.
Leptosiagon gracilis Owen: Etheridge Jun., 1878, p. 182; 1892, p. 674.
Pachysiagon ferragus Owen: Etheridge Jun., 1878, p. 186; 1892, p. 675.
Macropus ferragus Owen: Lydekker, 1887, pp. 230–1; Simpson, 1930, p. 72.
Macropus gracilis Owen: Simpson, 1930, p. 72.
?*Macropus (Macropus) ferragus* Owen: Tedford, 1967, pp. 127–43.

MATERIAL: F3865, cast of holotype *M. ferragus* Owen, British Museum (Natural History) number 32903, partial right mandibular ramus with M_2 shattered, M_3–M_4, adult, Condamine River, southeastern Queensland, apparently from Pleistocene fluviatile deposits (figd Owen, 1874, pl. 81, fig. 4; pl. 82, figs. 3–4; pl. 83, fig. 3; 1877, pl. 91, fig. 4; pl. 92, figs. 3–4; pl. 93, fig. 3).

F3867, cast of holotype *M. gracilis* Owen, British Museum (Natural History) number 40005, partial right mandibular ramus with M_2–M_3, juvenile, Queensland, apparently from Pleistocene fluviatile deposits (figd Owen, 1874, pl. 76, figs. 11–15; 1877, pl. 89, figs. 11–15).

Also referred to *M. ferragus* are 5 juvenile mandibular rami, 15 adult mandibular rami and 2 juvenile maxillae from the following localities in the Pleistocene fluviatile deposits: Ravensthorpe, Pilton; King Creek, Pilton, at M.R.098465 Liverpool Range 1-mile sheet; King Creek, near M.R.039454 Clifton 1-mile sheet; Macalister; Gowrie; and from the eastern Darling Downs (particular localities unspecified).

DIAGNOSIS: A large species, somewhat larger than *Macropus (Macropus) titan* Owen. Mandible narrow immediately below anterior cheek teeth and also deep in that area. P_3 small, with longitudinal crest trifid, with posterior cuspid and associated ridges offset and separated from anterior cuspid and mesial cuspule which are united by longitudinal crest. Lower molars with very high lophids, with anterior moiety in occlusal view rotated labially relative to posterior moiety about a point approximately one-half distance along labial base, producing broadly U-shaped part of talonid basin lingually and sharply V-shaped part of basin labially. Anterior cingulum very high, somewhat recurved, very broad; posterior of hypolophid with deep, moderately angled groove linguad to midline, flanked by ridges and reduced grooves; occasionally groove opens basally into strong posterior fossette. P^3 with longitudinal crest markedly concave labially and with one cuspule intermediate between paracone and metacone along crest; hypocone strongly defined, united to below metacone by anterolabial ridge; lingual cingulum anteriorly convergent, markedly tuberculate in lingual view, extending to anterior of base of crown. Upper molars with very broad, moderately high anterior cingulum, somewhat recurved; forelink extremely reduced; anterior portion of midlink crescentic; labial moiety of median valley in anterior molars with reduced ridge connecting paracone and metacone; posterolabial ridge from hypocone widely flared.

DESCRIPTION: mandible deep below anterior molars and in diastemal area, relatively thick posteriorly; base of symphysis deflected, near planar; symphysis relatively elongate, shallow, not ankylosed, rugose; geniohyal pit relatively deep, above posterior symphysial limit; diastema comparatively elongate, with diastemal crest posteriorly very acute, and with body of ramus very narrow below anterior cheek teeth; ventral margin of ramus rounded between symphysis and extremely weak digastric ridge and process. Mental foramen moderately large, oval, below diastemal crest, anterior to anterior root of P_3. Ramus with very shallow lateral groove extending posteriorly to below anterior M_2, close to alveolar margin. Digastric process separated from base of angle by shallow post-digastric sulcus, bounded above by shallow digastric fossa; this fossa separated above from broad depression leading posteriorly into pterygoid fossa. Post-alveolar shelf long, with angle not well-developed, leading to post-alveolar ridge, ascending posteriorly to disappear on mesial wall of coronoid process, above large mandibular foramen. Masseteric crest raised to about level of occlusion of cheek teeth; masseteric foramen moderately large, with masseteric fossa relatively deep. Bulk of angle of mandible, coronoid process and condyle not preserved in any specimen.

I_1, P_2 and DP_3 not preserved.

P_3 small, short, subovate in occlusal view, with labial margin slightly convex, and lingual margin somewhat concave. Crest trifid in lateral view. Anterior cuspid well-defined, with anterior ridge descending to crown base; posterior ridge descends as longitudinal crest uniting with anterior ridge

TABLE 8: SUMMARY OF MANDIBULAR MEASUREMENTS FOR *Macropus (Osphranter) ferragus* OWEN

Character	n	O.R.	$\bar{X}$	s	V
P_3 length	1	—	9·0	—	—
max. width	1	—	4·0	—	—
M_1 length	—	—	—	—	—
prot. width	2	7·9–8·7	8·3	—	—
M_2 length	8	16·0–17·8	16·9	0·7111	4·21
prot. width	8	9·1–10·1	9·7	0·3379	3·48
M_3 length	18	17·0–19·9	18·8	0·8095	4·31
prot. width	16	10·2–12·1	11·1	0·5279	4·76
M_4 length	13	19·4–22·4	20·8	0·8170	3·93
prot. width	13	10·4–12·6	11·4	0·6939	6·08

prot. = protolophid.

from well-defined mesial cuspule, above vertical labial and lingual ridges; posterior ridge from cuspule curves lingually to short groove at posterior one-quarter. Posterior cuspid with strong anterolabial ridge descending to strong groove at posterior one-third; a strong ridge descends posterolingually from posterior cuspid to base of crown; slight cuspule occasionally present along this ridge, just below cuspid. Labial base of crown slightly swollen.

$M_1 < M_2 < M_3 < M_4$; molars subrectangular in basal outline, somewhat constricted across talonid basin; lophids very high, with hypolophid crest more convex posteriorly than protolophid crest in unworn teeth, nearly similar in worn examples; hypolophid broader than protolophid in M_1, about equal in M_2 and M_3 and narrower in M_4. Trigonid basin very broad, its length being about equal to distance between lophids. Forelink very high, curving anterolingually from protoconid to point labiad to mid-line of very high somewhat recurved anterior cingulum. Cingulum with anterolabial indentation, very squared in appearance being inflated anterolingually and anterolabially; trigonid markedly sloping posteriorly from cingulum and descending slightly labially and lingually from forelink; slight anterolabial fossette usually present. Strong, high ridge curves anterolingually from hypoconid across talonid basin as midlink, uniting with short ridge from labiad to mid-point of protolophid; junction frequently flexed in unworn teeth. Talonid basin descends slightly labially and lingually from midlink; basin V-shaped labially, broadly U-shaped lingually, associated with strong labial flexure of crown about a point approximately mid-way along labial margin; slight groove usually present at crown base, near posterolabial margin of base of protolophid; slight ridges usually descend anteriorly and posteriorly from metaconid. Lingual moiety of talonid frequently with transverse fold to tooth margin; fold occasionally ascends posterior surface of protolophid, near junction with midlink. Posterior of hypolophid with well-defined somewhat oblique groove, linguad to mid-line, very occasionally leading into well-defined posterolingual fossette. Slight ridges flank groove, and usually very slight grooves present beyond ridges; occasionally posterolabial crown base marked by several radiating grooves. Base of crown broadly extended posteriorly, sometimes slightly swollen particularly at margins of talonid base. Labial bases of lophids more expansive than lingual. Cranium known only from fragmentary maxillary remains.

I^1–I^3, P^2, DP^3, M^4 not preserved.

P^3 relatively small, subovate in occlusal view, with labial margin slightly concave, and with lingual margin convex. Paracone well-defined with strong anterior ridge ascending towards crown base where it curves lingually; posterior paracone ridge contributes to longitudinal crest. Crest trenchent, somewhat concave labially. Metacone reasonably well-defined, with anterior ridge extending as crest and with posterior ridge curving lingually above crown base to unite with labially curving ridge ascending from hypocone; metacone positioned at posterior one-third; longitudinal crest transected by one slight set of vertical labial and lingual ridges with production of cuspule at crest. Hypocone with low antero-labial ridge connecting with slight vertical ridge ascending from metacone, delimiting broad, shallow, posterior fossette; anterior ridge from hypocone ascends to above crown base as lingual cingulum; cingulum convergent anteriorly, marked by strong tuberculation where extension of ridge from crest cuspule unites; vertical ridge from paracone unites with cingulum at anterior tuberculation, but cingulum extends further, to unite with anterolingually curving ridge from paracone at anterior

TABLE 9: MEASUREMENTS FOR *Macropus (Osphranter) ferragus* OWEN, MAXILLA

Specimen	P^3	M^1	M^2	M^3	M^4
F3720	13·0 × 6·4	—	15·1 × —	16·9 × 11·9	—
F1691	—	—	—	—	17·9 × 12·5

of crown. Lingual basin shallow, with transverse ridging slight. Base of crown somewhat swollen.

$M^1 < M^2 < M^3$; molars subrectangular in occlusal view, slightly constricted across median valley; lophs high, with metaloph crest more concave posteriorly than protoloph crest in unworn teeth, but nearly similar in worn examples; metaloph broader than protoloph in M^1, approximately equal in M^2 and M^3. Anterior cingulum relatively high, very broad, moderately short, overturned in unworn examples; forelink very weak, labiad to mid-line, frequently with no trace remaining in worn teeth; anterior cingular shelf less sloping lingually in labial moiety than lingual, strongly sloping posteriorly. Weak ridge ascends from paracone to labial extremity of anterior cingulum, separated from it by cleft. Midlink strong, high, ascending posteriorly from protocone in lunate form, uniting with slight ridge from near mid-point of metaloph, this ascending from near centre of metaloph crest; junction occasionally flexed; posterior ridge from paracone weak, ascending posteriorly to near base of median valley, then curving abruptly lingually before crossing valley to unite with equally weak, and similarly developed ridge from metacone; these ridges strongest in anterior molars; median valley slopes slightly labially and lingually from midlink, sharply U-shaped in labial moiety, V-shaped lingually; slight ridge usually delimits lingual extremity of median valley. Posterior ridge from hypocone strong, somewhat flared, ascending and curving labially to unite with much weaker ridge from metacone near posterolabial base of crown; well-developed posterior fossette present; posterolingually, broad groove normally descends from crown base, reaching hypocone ridge.

DISCUSSION: Tedford (1967) has very adequately presented evidence for the synonymy of *Macropus gracilis* Owen with *M. ferragus* Owen, a conclusion previously reached by Lydekker (1887). The mandible of the holotype of *M. ferragus* is poorly preserved. Excessive width of the ramus appears to be the result of fragmentation and wedging by calcite. This may have been combined with a primary abnormality in width. As a result, this character is of doubtful worth although Owen (1874) considered width of the mandible to be diagnostic of the species. Morphologically, the molars of the holotypes of *M. gracilis* and *M. ferragus* are generally similar, differing mainly in the structure of the posterior surface of the hypolophid, a feature which shows some variation in the Queensland sample of *M. ferragus*. Grooving of the posterior hypolophid surface of the molars of the *M. gracilis* holotype is most commonly represented in the present sample. Owen (1874) stressed this feature in his description of *M. gracilis*, and regardless of some variation in this character, the synonymy is considered justifiable.

From Tedford's (1967) description and figures of *M. ferragus* it is evident that a mixed sample is involved in the Lake Menindee material. Tedford argued that high values for the Coefficient of Variation in that sample probably resulted from variable inter-tooth attrition, true variation patterns, and possibly sexual differences. Values of this order, up to V = 13·26 in the posterior width of M_4, are unknown in related fossil macropodines and are completely at variance with control statistical results reported by Bartholomai (1971) and with values for V for the present sample of *M. ferragus*. Further, while slight sexual differences are evident in the recent control samples, no marked separation occurs in the characters considered and only insignificant bimodality occurs in the histograms. Some overlap in measurements is evident in Tedford's (1967) sample with those of *M. titan* presented in the present study (Table 1). It would appear that material very similar morphologically to *M. titan* has contributed to Tedford's description of *M. ferragus*. This is supported by the morphology of premolars figured and described by Tedford.

Compared with the values presented in Table 8, a summary of mandibular measurements for *M. ferragus* from Queensland, Tedford's (1967) Lake Menindee sample overlaps considerably. These frequently exceed values for the present material in observed ranges of cheek teeth. Thus, while some Lake Menindee material may be referable to *M. ferragus* some may be separable from both *M. titan* and *M. ferragus*. For this reason, the specific identity of the post-cranial remains referred to *M. ferragus* by Tedford is uncertain, but they are undoubtedly referable to the genus *Macropus*.

Mandibular and maxillary remains of *M. fer-*

ragus have not been located together but the present association is considered correct. Occlusion is satisfactory and morphological features in upper and lower dentitions are compatible. *M. ferragus* is not common in the Darling Downs deposits and statistical evaluation has been limited to posterior lower molars. Measurements for referred maxillary remains are presented in Table 9.

Lydekker (1887) referred a partial palate and portion of a left maxilla from the Condamine River, Queensland, to this species, differentiating these from *M. titan* Owen by their slightly larger size and more complex molars. Lydekker also referred a partial mandible and maxilla from the Pleistocene of Kirban, Mendoran, New South Wales, stating that the molars of the mandible agree precisely with those in the holotype of *M. gracilis*.

M. ferragus is distinguished from *M. titan* by the structure of both molars and premolars, and to some extent by the structure of the lower jaw. While P_3 in *M. titan* does achieve a trilobate appearance in extreme variants, the posterior lobe is never detached and angled to the general line of the longitudinal crest. Further, the lower molars are normally marked by a well-defined posterior fossette and a lower anterior cingulum, while the ramus is shallower in the diastemal area and is not so markedly compressed immediately below the anterior cheek teeth. Upper premolars in *M. titan* lack a lingual cingulum and have a cleft longitudinal crest, while upper molars in *M. titan* lack a recurved anterior cingulum and possess a strong forelink.

The log difference diagram presented in Fig. 2 indicates marked differences in relative proportions of mean values for cheek teeth in *M. ferragus* compared with those in *M. pan* from the Chinchilla Sand, described below. The permanent premolars are comparatively longer while the last lower molar

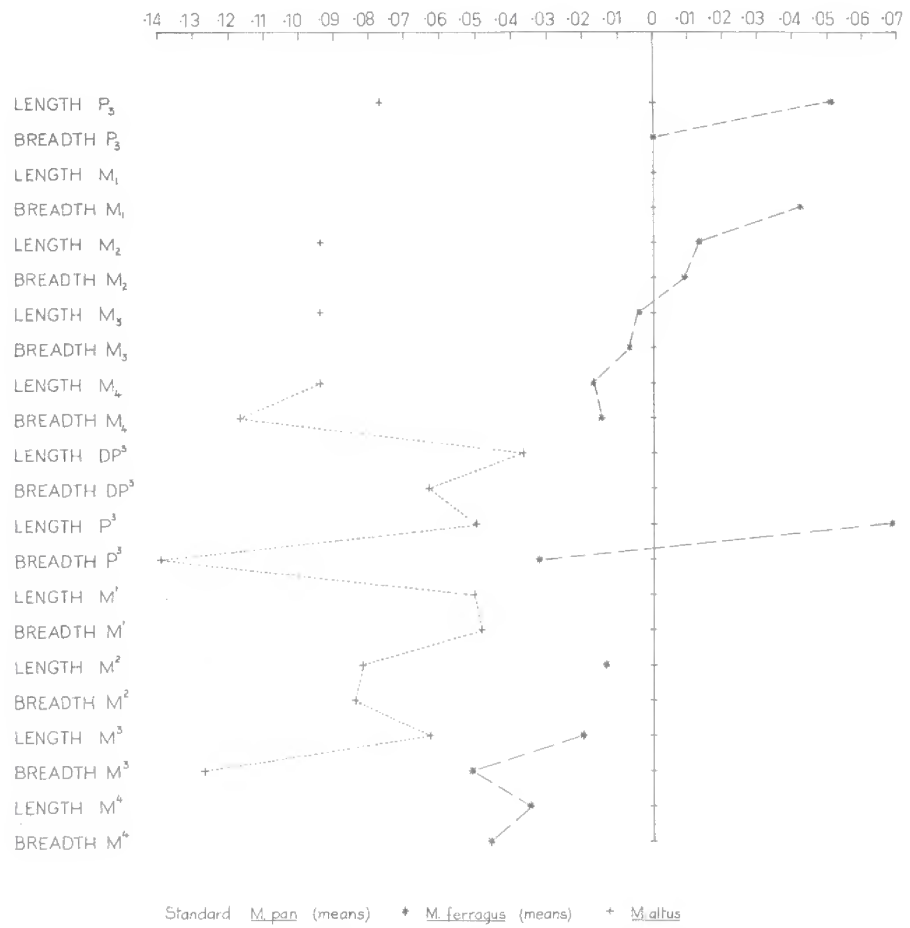


FIG. 2: Log Difference Diagram illustrating relative proportional differences in cheek-teeth in *M. ferragus*, *M. altus*, and *M. pan*.

is relatively smaller compared with M_3. Comparison of the upper dentition is less conclusive, because it is based on a small sample in *M. ferragus*. This figure also presents details for *M. altus*, which compares more closely with *M. ferragus*, although again a very small sample is involved. *M. altus* is readily distinguished from *M. ferragus* by its much smaller size and by minor morphological details.

Macropus (Osphranter) pan De Vis, 1895
(Plate 16, figs. 1–4; Plate 17, figs. 1–4; Plate 18, figs. 1–2)

Macropus pan De Vis, 1895 *(partim)*, pp. 124–7, figs. 7, 9–10; *non* fig. 8; Simpson, 1930, p. 72; Bartholomai, 1966, pp. 124–5, pl. 18, figs. 4–6.

MATERIAL: F2925, holotype, partial right maxilla with DP^3–M^2, juvenile, Darling Downs (figd Bartholomai 1966, pl. 18, figs. 4–6); preservation indicates derivation from the late Pliocene Chinchilla Sand.

Also referred to *Macropus pan* from the collections of the Queensland Museum are a juvenile maxilla, 11 adult maxillae, 21 isolated upper molars, 34 juvenile mandibular rami, 23 adult mandibular rami and 23 isolated lower teeth from the following localities: Chinchilla, SE.Q.; Condamine River, 60 m east of eastern boundary of Chinchilla Rifle Range (Rifle Range No. 78, Par. of Chinchilla), SE.Q.; Condamine River, c. 5 km southeast of Chinchilla, SE.Q.; near M.R.363676 Chinchilla 4-mile sheet; and from the western Darling Downs (particular localities unspecified).

DIAGNOSIS: P_3 relatively large, with well-defined, short, low, lingual cingulum and with high, longitudinal crest transected by one vertical set of labial and lingual ridges; small posterolingual fossette present. Upper molars with high lophs, somewhat rotated; forelinks moderately well-defined and midlinks high. Labial portion of median valley with low accessory link, becoming weaker or absent in posterior molars. Mandible large; P_3 relatively small, usually presenting distinct posterolingual cuspid; longitudinal crest normally trifid, ascending posteriorly, usually transected mesially by set of vertical labial and lingual ridges. Lower molars with high, somewhat rotated lophids, and relatively high anterior cingulum and forelink; midlink high; posterior of hypolophid with slight oblique groove to base of crown; posterior fossette normally absent.

DESCRIPTION: I^{1-3}, and P^2 unknown.

DP^3 molariform, too worn to be adequately described. Semblance of accessory link present in labial moiety of median valley.

P^3 relatively large, subovate in basal outline, broader posteriorly. High, relatively short longitudinal crest transected by median vertical set of labial and lingual ridges, with production of cuspule at crest. Moderately high hypocone close to metacone, connected to above metacone by labial ridge; posterior ridge from hypocone curves posterolabially below base of crown to unite with posterior ridge from metacone, with production of well-defined posterolingual fossette; anterior ridge from hypocone ascends to unite with base of crown, linguad to paracone, as low lingual cingulum: cingulum with well-defined but low tuberculation; lingual basin narrow, moderately shallow. Low, broad ridge crosses lingual basin from tubercle on cingulum.

$M^1 < M^2 < M^3 < M^4$; molars subrectangular in basal outline, slightly constricted across median valley, particularly in posterior molars. Lophs very high in unworn teeth, anteriorly bowed, somewhat rotated in lateral and occlusal view; metaloph broader than protoloph in M^1, almost equal in M^2, and slightly narrower in M^3 and M^4. Anterior cingulum relatively high and moderately narrow, short; forelink generally well-defined and strong but variable, passing posteriorly from near mid-point of anterior cingulum to point linguad to centre of protoloph. Lingual moiety of anterior cingular shelf ascending sharply; labial moiety ascending slightly from forelink with occasional production of shallow anterolabial fossette. Variable ridges ascend anteriorly and posteriorly from paracone. Midlink high, strong, ascending labially from protocone then posteriorly across median valley to unite with short ridge from near mid-point of metaloph; junction often marked by vertical grooves and flexure; median valley V-shaped, sometimes partially delimited labially by low, variable ridges on posterior surface of protoloph and anterior surface of metaloph. Anterior ridge from metacone weak, variable, generally ascending into median valley as accessory link across labial moiety of valley, this link becoming reduced or absent in posterior molars; accessory link often unites with weak posterior ridge from paracone; posterior surface of protoloph between midlink and ridge to accessory link broadly swollen. Well-defined ridge ascends posterolabially from hypocone to unite basally with slight variable posterior surface of diagonal ridge from hypocone generally grooved parallel to margin of ridge. Mandible elongate, strong, moderately deep and posteriorly broad. Symphysis relatively shallow, not ankylosed; geniohyal pit moderately deep. Diastema long, crest acute; ramus deep in diastemal area. Mental foramen relatively large, oval, set just below diastemal crest. Ramus narrow and grooved laterally from below anterior extent of

tooth row to position about one-half way along alveolar margin. Ventral margin of ramus broadly rounded posterior to symphysis, with digastric process weak; digastric fossa separated above from broad lingual depression opening posteriorly into pterygoid fossa. Post-alveolar shelf moderately long, leading to mesial surface of coronoid process. Most of coronoid process and angle of mandible not preserved.

I_1 and P_2 not preserved in any specimen.

DP_3 molariform, relatively small, much narrower anteriorly than posteriorly, only slightly constricted across talonid basin in some individuals. Lophids high, somewhat variably rotated forward. Trigonid basin relatively broad, its length almost equalling distance between lophids. Forelink strong, moderately high, descending across trigonid basin from protoconid to point well labiad of mid-point of moderately high anterior cingulum, almost at anterolabial margin of tooth. Talonid basin sharply U-shaped lingually and V-shaped labially. Midlink high, strong, descending from hypoconid across talonid to point well labiad to mid-point of posterior surface of protolophid. Moderately shallow diagonal groove descends from near hypoconid, to near posterolingual margin of crown.

P_3 relatively small, subtriangular in basal outline. Longitudinal crest secant, usually transected mesially by set of vertical labial and lingual ridges with the production of cuspule at crest; mesially, cuspule occasionally not developed; crest somewhat concave labially, variably ascending posteriorly. Small subsidiary cuspid developed posterolingually, close to crest, sometimes below and sometimes at same level as posterior cuspid of crest; separated from crest by anterior and posterior grooves, usually linked by short ridge. Base of crown slightly swollen.

$M_1 < M_2 < M_3 \leq M_4$; molars subrectangular in basal outline, somewhat constricted across talonid basin, particularly in posterior molars. Lophids very high, somewhat rotated in unworn teeth, with protolophid narrower than metalophid in M_1 and M_2 and slightly broader in M_3 and M_4. Trigonid basin relatively broad but somewhat variable, its length almost equalling distance between lophids. Forelink high, strong, descending anterolingually from protoconid to point somewhat labiad of mid-point of moderately high anterior cingulum near mid-point. Forelink occasionally ornamented labially by low accessory fold. Labiad moiety of trigonid basin often with development of anterolabial fossette; trigonid descends variably on each side of forelink. Protolophid crest often distorted mesially in unworn teeth, while hypolophid crest often subdivided mesially by short vertical grooves. Midlink high, strong, descending anterolingually then anteriorly from hypoconid to unite above talonid basin with short ridge from near mid-point of protolophid; lingual moiety of talonid basin U-shaped, labial moiety V-shaped; low accessory link variably present in lingual moiety of talonid basin in M_1. Posterior surface of hypolophid with shallow diagonal groove from near hypoconid to near posterolingual margin of crown. Posterior fossette normally absent.

DISCUSSION: *Macropus (Osphranter) pan*, described by De Vis (1895), was one of the few species for which he designated a holotype. This specimen, a juvenile maxilla, F2925, redescribed and figured by Bartholomai (1966), unfortunately lacks locality information other than Darling Downs. Preservation suggests it came from the Chinchilla Sand of late Pliocene age. The species appears to be restricted to that Formation. The material referred by De Vis (1895) to *M pan* now appears to have also included *M. ferragus* Owen. Specimens referable to both species were figured by De Vis (1895, pl. 18, figs. 7–10). Of these, the subject of fig. 8, is the P^3 of F3720, here referred to *M. ferragus*.

M. pan and *M. ferragus* are morphologically similar, particularly in the permanent upper and lower premolars. P^3 in *M. ferragus* is a relatively more elongate tooth with a stronger lingual cingulum, while P_3 in *M. ferragus* is more definitely trifid, with the posterior lobe offset from the general line of the longitudinal crest. No well-defined internal cuspid is developed. Upper molars in *M. ferragus* lack well-defined forelinks but possess vestigial accessory links in anterior molars, a structure well-developed in *M. pan*. In lower molars, the main distinction occurs on the posterior surface of the hypolophid. *M. pan* normally has an oblique groove, while *M. ferragus* has a near vertical groove, flanked by accessory ridges. A posterior fossette is rarely present in both species but tends to be present more frequently in *M. ferragus*. Differences in relative proportions of cheek teeth between *M. pan* and *M. ferragus* are presented in Fig. 2.

Material exists in the Chinchilla Sand which is somewhat similar to *M. pan* but which possesses a widely flaring posterior fossette at the base of the posterior groove in the molars. These specimens, F5445 and F5449, could represent extreme variation in *M. pan*.

Although cranial remains have not been located together, the present association is considered correct. Occlusion is satisfactory and the basically similar morphology in the referred upper and lower

TABLE 10: SUMMARY OF MEASUREMENTS IN *Macropus(Osphranter) pan* DEVIS

Character	Maxillae					Mandibles				
	n	O.R.	$\bar{X}$	s	V	n	O.R.	$\bar{X}$	s	V
DP^3_3 length	1	—	10·6	—	—	6	10·1–11·5	10·7	0·496	4·63
prot. width	1	—	8·1	—	—	6	5·1– 5·8	5·4	0·340	6·31
P^3_3 length	1	—	11·1	—	—	8	6·5–10·1	8·0	1·104	13·80
max. width	1	—	6·9	—	—	8	3·3– 4·6	4·0	0·492	12·31
M^1_1 length	4	11·7–13·8	12·8	—	—	20	12·4–14·5	13·5	0·542	4·01
prot. width	2	10·0–10·7	10·4	—	—	18	6·5– 8·1	7·5	0·418	5·58
M^2_2 length	13	14·6–16·3	15·6	0·477	3·06	27	15·0–17·2	16·4	0·566	3·45
prot. width	12	11·6–13·6	12·5	0·566	4·53	25	8·1–10·7	9·5	0·591	6·22
M^3_3 length	18	16·2–18·8	17·7	0·730	4·13	32	17·9–20·3	19·0	0·587	3·09
prot. width	17	12·5–14·3	13·4	0·488	3·64	30	10·2–12·5	11·3	0·552	4·88
M^4_4 length	11	18·2–20·1	19·4	0·347	1·78	27	20·0–23·1	21·6	0·716	3·31
prot. width	9	13·0–14·5	13·9	0·475	3·42	26	10·8–12·7	11·8	0·515	4·36

prot. = protoloph or protolophid.

remains supports this. No post-cranial material has been referred from the Chinchilla Sand collections.

De Vis (1899b) recorded *M. pan* cranial material from Lake Colongulac, Victoria. As indicated previously, this is most likely *M. titan*. From De Vis' descriptions, the skull material is totally unlike that here referred to *M. pan*, and the anterior upper molars lack the characteristic accessory link present across the median valley. Similarly, the lower premolars are bifid, with a posterolingual cuspid, as in *M. titan*.

Of recent species, the wallaroos, *M. antilopinus* and *M. robustus* are morphologically similar to *M. pan*, with the same basic structure present in the cheek teeth and lower jaw. This similarity is less evident than that between *M. ferragus* and *M. altus* and these recent species. A strong lingual cingulum in P^3 is common to all, as are the relatively high, somewhat rotated molar lophs and lophids and grooved hypolophids.

Summaries of mandibular and maxillary measurements for the *M. pan* sample are presented in table 10. They indicate values for the Coefficient of Variation similar to those for other Queensland fossil and living macropodids. Only the size of P_3 shows excessive values for V. As in other species, this is believed to indicate true variation rather than mixing of samples or sexual differences.

M. pan represents the most common species of *Macropus* in the Chinchilla Sand and is the largest grazing macropodine recovered from that formation.

Macropus (Osphranter) woodsi* sp. nov.
(Plate 19, figs. 1–4; Plate 20, figs. 1–4)

MATERIAL: F3920, holotype, partial right mandibular ramus with P_3 erupting, M_1–M_2, M_3 erupting, juvenile, Condamine River end of Middle Gully system, Chinchilla Rifle Range (Rifle Range No. 78, Par. of Chinchilla), from the late Pliocene Chinchilla Sand.

Referred specimens in the collections of the Queensland Museum comprise F5460, partial right mandibular ramus with P_3–M_2, adult, Chinchilla; F40 partial right mandibular ramus with M_3–M_4, Warra; F5459, partial right mandibular ramus with M_4, adult, western Darling Downs; F5452, partial left mandibular ramus with P_3–M_4, adult, western Darling Downs; F5466, partial right mandibular ramus with M_1, P_3 removed by fenestration, upper limits of middle gully system, Chinchilla Rifle Range (Rifle Range No. 78, Par. of Chinchilla); F5453, partial left mandibular ramus with M_3–M_4, adult, western Darling Downs; F5454, partial right mandibular ramus with M_3, M_4 erupting, juvenile, western Darling Downs; F3631, partial right mandibular ramus with M_4, adult, Chinchilla; F5457, partial right mandibular ramus with M_3–M_4, adult, western Darling Downs; F5458, partial left mandibular ramus with M_4, adult, Western Darling Downs; F5451, partial left mandibular ramus with M_3–M_4, adult, western Darling Downs; F5461, partial left mandibular ramus with M_4, adult, Chinchilla; F5463, partial right mandibular ramus with M_4, adult, Chinchilla; F5464, partial right mandibular ramus with M_4 erupting, juvenile, Condamine River, at M.R.363675 Chinchilla 4-mile map; F5446, partial right mandibular ramus with M_2, P_3 removed by fenestration, juvenile, western Darling Downs; F5468, partial right mandibular ramus with all

* Named for Mr. J. T. Woods, in recognition of his contributions to the knowledge of the vertebrate fossils of Queensland.

teeth lost, adult, middle gully system, Chinchilla Rifle Range (Rifle Range No. 78, Par. of Chinchilla); F6090, isolated M_4, juvenile, western Darling Downs; F6091, isolated M_4, adult, western Darling Downs.

F5462, partial left maxilla with M^3–M^4, adult, Chinchilla; F5465, partial left maxilla with M^2–M^4, adult, Chinchilla Rifle Range, at M.R.363677 Chinchilla 4-mile map; F3718, partial right maxilla with M^2–M^4, adult, western Darling Downs; F5455, partial left maxilla with M^3–M^4, adult, western Darling Downs.

DIAGNOSIS: A small species, with ramus shallow, moderately wide; P_3 relatively elongate, having longitudinal crest transected mesially by broad, vertical set of labial and lingual ridges, and usually curving posterolingually in posterior one-third; crest ascends posteriorly. Lower molars with high, somewhat rotated lophids; links frequently labiad to mid-line, while posterior hypolophid surface marked by relatively strong, oblique groove, linguad to axis of crown. Upper molars with relatively strong links; labial moiety of median valley frequently crossed by low accessory link, this often well-developed even in posterior molars.

DESCRIPTION: Mandible shallow, relatively wide; base of symphysis inclined slightly at about 5° to base of mandible, somewhat deflected posteriorly; symphysis elongate, shallow, rugose, not ankylosed; geniohyal pit shallow, at posterior symphysial limit; diastema elongate with crest acute; ventral margin of ramus rounded between symphysis and weak digastric process. Mental foramen small, ovate, situated below digastric crest, well anterior to P_3. Ramus with shallow lateral groove developed from below P_3 to below posterior root M_3, at some distance below alveolar margin. Digastric process separated from base of angle by very shallow post-digastric sulcus, bounded above from shallow depression opening posteriorly into pterygoid fossa. Post-alveolar shelf short, with angle poorly developed, leading to post-alveolar ridge, ascending posteriorly to disappear on mesial wall of coronoid process, above large mandibular foramen. Masseteric crest raised to slightly below level of occlusion of cheek teeth. Bulk of coronoid process, angle of mandible and condyle not preserved in any specimen.

I_1 and P_2 unknown; DP_3 known only in fractured state.

P_3 relatively elongate, subcrescentic to subovate in basal outline, frequently convex labially and concave lingually. Longitudinal crest trenchant, with anterior cuspid well-defined but with posterior cuspid less well-defined; crest ascends posteriorly, being transected mesially by broad set of vertical labial and lingual ridges, with production of cuspule at crest, giving crest trifid appearance in lateral view; posterior one-third of crest usually curves posterolingually before descending to crown base, rarely offset and rarely with posterolingual cuspid developed. Base of crown slightly swollen.

$M_1 < M_2 < M_3 < M_4$; molars subrectangular in basal outline, slightly constricted across talonid basin; lophids high, convex posteriorly, somewhat anteriorly rotated in labial view, with hypolophid broader than protolophid in M_1 and M_2, approximately equal in M_3 and narrower in M_4. Trigonid basin relatively broad, its length approximately equalling distance between lophids. Forelink high, curving anterolingually from protoconid across trigonid basin to point labiad to mid-line on high, somewhat overturned anterior cingulum; trigonid slopes labially and lingually from forelink, and posteriorly from cingulum; anterior cingulum more expanded and angular anterolingually; slight ridge descends anteriorly from metaconid; slight anterolabial fossette developed in trigonid. Posterior ridge from metaconid very weak. Midlink high, strong, curving anterolingually from hypoconid to unite with short ridge from point labiad to mid-line, above talonid basin; junction often flexed; talonid basin sharply V-shaped labially, broadly U-shaped in lingual moiety; basin slopes labially and lingually from midlink, often ornamented by broad, low fold from hypolophid into lingual extremity; anterior and posterior ridges from entoconid weak. Posterior of hypolophid with moderate, oblique groove, developed linguad to axis of crown; M_4 often with posterior fossette developed at base of groove. Crown somewhat flexed about labial extremity of talonid, usually with subsidiary vertical groove developed at posterolabial base of protolophid; accessory vertical grooves occasionally present on labial portion of posterior of hypolophid.

TABLE 11: SUMMARY OF MAXILLARY MEASUREMENTS FOR *Macropus (Osphranter) woodsi* SP. NOV.

Character	n	O.R.	$\bar{X}$	s	V
M^2 length	1	—	14·0	—	—
M^3 length	4	14·1–16·1	15·2	0·787	5·18
prot. width	2	11·7–12·2	12·0	—	—
M^4 length	4	15·7–17·1	16·4	0·622	3·79
prot. width	4	12·1–12·7	12·3	0·264	2·15

prot. = protoloph.

Cranium known only from fragmentary maxillary specimens.

I^{1-3}, P^2, DP^3 and M^1 unknown.

$M^2 < M^3 < M^4$; molars subrectangular in basal outline, slightly constricted across median valley;

lophs moderately high, anteriorly bowed, somewhat rotated anteriorly in labial view; metaloph slightly broader than protoloph in M^2, approximately equal in M^3 and narrower in M^4. Anterior cingulum relatively low, broad, short, nearly horizontal in labial moiety, descending lingually; forelink well-developed, near axis of crown; cingulum usually united to base of protoloph delimiting anterolabial fossette; anterior paracone ridge very slight. Midlink high, strong, curving posterolabially from protocone across median valley to unite with short ridge from near mid-point of metaloph; junction occasionally flexed. Median valley near horizontal transversely, sometimes excavated between midlink and limit of valley, V-shaped labially and lingually; posterior ridge from paracone and anterior ridge from metacone weak, usually uniting across median valley as accessory link, paralleling midlink; this often developed even in M^4. Strong, flared ridge curves posterolabially from hypocone to posterolabial base of crown, uniting with slight ridge ascending posteriorly from metacone; well-defined posterior fossette developed between these and posterior, broadly grooved surface of metaloph.

DISCUSSION: At present, *Macropus woodsi* is recorded only from the late Pliocene Chinchilla Sand but it is reasonably well represented. Although incompletely known, enough is preserved to justify separation from *M. pan*, the dominant species of *Macropus (Osphranter)* in the Chinchilla Sand, which it resembles in general morphology. *M. woodsi* is the smaller of the two species, in both size of cheek teeth and dimensions of the mandibular ramus.

This size difference is not believed to represent sexual dimorphism in a single species, although it has been shown by Bartholomai (1971) that sexual dimorphism in the dentition of certain larger living macropodids may be significant. No comparable work, similar to that presented in Bartholomai (1971) has been undertaken for wallaroos but examination of sexed samples of *M. robustus* and *M. antilopinus* suggests that sexual dimorphism in the cheek teeth, if present, is not as great as size differences observed between *M. pan* and *M. woodsi*. Further, *M. woodsi* is considerably less well represented than *M. pan*. Should the differences comprise sexual dimorphism, approximately equal numbers of larger and smaller individuals would be expected in the sample because of approximately equal numbers of each sex in living species (Bartholomai, 1971). Size differences in lower molars between *M. woodsi* and *M. pan* are graphically represented in Fig. 3.

TABLE 12: SUMMARY OF MANDIBULAR MEASUREMENTS FOR *Macropus (Osphranter) woodsi* SP. NOV.

Character	n	O.R.	$\bar{X}$	s	V
P_3 length	5	7·5– 9·1	8·1	0·592	7·30
max. width	4	4·1– 4·9	4·3	0·387	9·00
M_1 length	5	10·4–12·3	11·4	0·973	8·53
prot. width	5	6·9– 7·6	7·2	0·308	4·28
M_2 length	3	13·5–14·9	14·0	0·758	5·42
prot. width	5	8·1– 9·1	8·5	0·331	3·89
M_3 length	5	15·2–16·5	16·0	0·570	3·56
prot. width	6	9·0–10·5	9·8	0·500	5·10
M_4 length	14	17·2–18·8	18·1	0·550	3·04
prot. width	14	9·6–10·8	10·0	0·404	4·04

prot. = protolophid.

A summary of mandibular measurements for *M. woodsi* is provided in Table 12. Coefficients of Variation are in keeping with those expected for a sample from a fossil species, taking into account the limited size of the sample examined. A summary of measurements for the small maxillary sample is provided in Table 11.

Mandibular and maxillary remains of *M. woodsi* have not been located together but occlusion and morphological compatibility of upper and lower dentitions indicate the correctness of the present association.

In addition to its smaller size, *M. woodsi* differs from *M. pan* in having a posterior fossette at the base of the oblique posterior hypolophid groove in M_4, and in normally lacking a posterolingual cuspule in P_3. The upper molars present in *M. woodsi* have similar accessory links in the lingual moiety of the median valley, but these are frequently well-developed in posterior molars as well as anterior molars. The occasionally offset posterior lobe of P_3 in *M. woodsi* is more like that developed in *M. ferragus* than in *M. pan*, but the posterior hypolophid groove in lower molars differs considerably from that in *M. ferragus*, where this groove is usually near vertical and flanked by lateral ridges.

Macropus (Prionotemnus) agilis siva (De Vis, 1895)
(Plate 21, figs. 1–4; Plate 22, figs. 1–3)

Halmaturus siva De Vis, 1895, pp. 113–4, pl. 17, figs. 21–22.
Halmaturus cooperi (Owen): De Vis, 1895 *(partim)*, pp. 116–8.
Macropus siva (De Vis): Simpson, 1930, p. 73.
'Halmaturus' siva De Vis: Bartholomai, 1966, pp. 118–9, pl. 16, figs. 4–6.

MATERIAL: F2926, holotype, partial right mandibular ramus with P_3, M_2–M_4, adult, Darling Downs, south-eastern Queensland (redescribed and figured by Bartholomai, 1966, pl. 16, figs. 4–6).

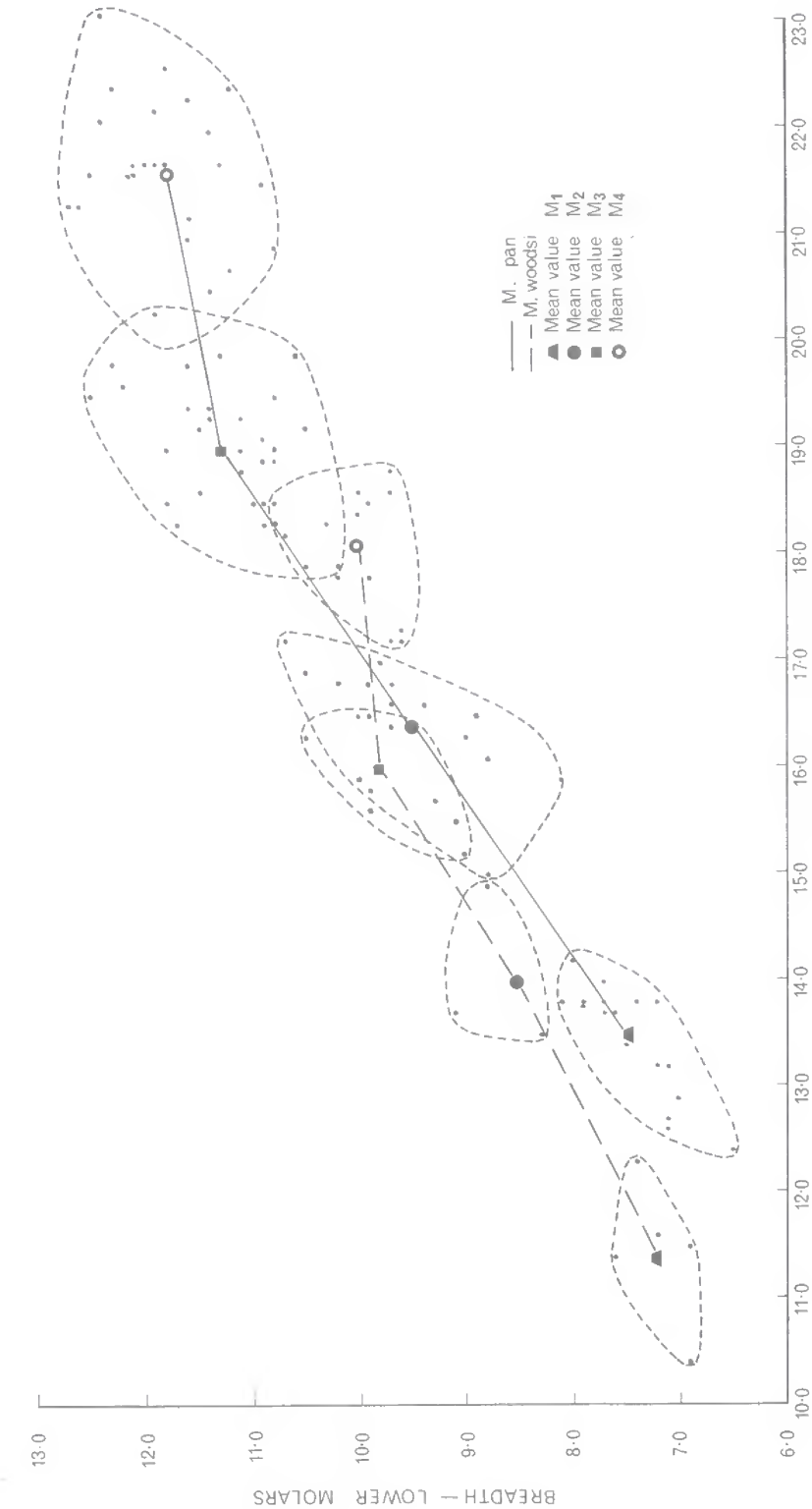


FIG. 3: Scatter diagram comparing lower molar teeth in *Macropus (Osphranter) woodsi* with *M. pan*. Lines have been added joining mean values.

In addition, 45 partial juvenile mandibular rami, 41 partial adult mandibular rami, one partial adult cranium, one premaxillary fragment, four juvenile maxillae and three adult maxillae have been referred to this subspecies from the following localities in the Pleistocene fluviatile deposits of the eastern Darling Downs: King Creek, near M.R.047452 Clifton 1-mile sheet; King Creek, Pilton; Ravensthorpe, Pilton; King Creek, near M.R.039454 Clifton 1-mile sheet; King Creek; ?Ravensthorpe, Pilton; King Creek, at bridge on Pratten road, at M.R.863331 Clifton 1-mile sheet; ?Pilton; Clifton; Freestone Creek; ?Freestone Creek; gravel below Freestone State School, Freestone Creek; Gowrie Creek; Gowrie; ?Gowrie; Jimbour Creek, near Dalby; Jimboomba; Spring Creek, Clifton; eastern Darling Downs, and from unspecified localities within the Darling Downs, but with specimens possessing preservation in keeping with derivation from eastern Darling Downs deposits.

One maxillary fragment is referred to *M. agilis siva* from 67 feet in a creek bed at Monto, southeastern Queensland.

DIAGNOSIS: Relatively large compared with living *Macropus agilis*. Ramus with elongate diastema, and with P_3 approximately as long as M_1; P_2 relatively elongate; lower molars with high lophids and moderately high links; posterior cingulum not developed.

Upper premolars elongate; upper molars with high lophs, slight forelink and moderately high midlink; ridge from paracone to labial extremity of anterior cingulum strong. Incisive foramina originate mid-way between I^3 and premaxilla–maxilla suture; posterior palatine vacuities originate opposite M^3–M^4 at eruption of M^4.

DESCRIPTION: Mandible moderately strong, being relatively wide but shallow, with longitudinal axis markedly concave laterally. Symphysis elongate, not ankylosed, set at low angle to base of mandible; geniohyal pit insignificant. Diastema long; ventral margin of ramus sharply rounded posterior to symphysis, becoming more broadly rounded posteriorly; mental foramen moderately large, ovate, situated close to diastemal crest, approximately mid-way between anterior root P_3 and limit of ramus; mandible usually with shallow labial groove present close to alveolar margin from above mental foramen to below anterior of M_3. Digastric process extremely weak, separated from base of angle by slight post-digastric sulcus; shallow, broad depression present opening posteriorly into pterygoid fossa; post-alveolar shelf short, leading to post-alveolar ridge which disappears on mesial wall of moderately high coronoid process above large mandibular foramen; leading edge of process inclined at about 15° to vertical; condyle subtriangular, being moderately broad and long, slightly concave laterally. Tip of coronoid process and angle of mandible not preserved.

I_1 elongate, deeply rooted, slightly curved in lateral and occlusal views; wear facet with upper incisors sub-horizontal; mesial facet of wear present at tip by approximation with other lower incisor. Root compressed oval in section; crown subquadrantal in section, tapering and blade-like distally, enamelled laterally, this produced dorsolabially and ventrolingually into flanges.

P_2 relatively elongate, subcrescentric to subtriangular in basal outline. Longitudinal crest secant, curving lingually in its posterior extension and usually curving anterolingually but occasionally descending anteriorly from anterior cuspid. Crest transected by a major set of vertical, labial and lingual ridges at its anterior one-third and by a minor set of ridges at its posterior one-third, with production of cuspules at crest; anterior cuspule better defined. An accessory posterolingual cuspule occasionally present.

DP_3 molariform, subtriangular in basal outline; lophids high with hypolophid crest much broader than protolophid; both lophids markedly convex posteriorly in unworn teeth. Trigonid basin narrow, being particularly poorly developed labially, elongate, its length almost equalling distance between lophids. Forelink moderately high, strong, descending and slightly curving anterolingually then anteriorly or even anterolabially, from protoconid to point on moderately high anterior cingulum, well labiad to axis of crown. Variable accessory fold of enamel present in lingual portion of trigonid, usually close to and paralleling forelink; slight fossette formed in reduced labial moiety of trigonid. Moderately strong, short ridge descends posteriorly from protoconid to unite with moderately high midlink descending anterolingually from hypoconid. Talonid basin V-shaped in both labial and lingual moieties; labial portion much reduced. Anterior ridge from entoconid weak. Posterior of hypolophid rounded, unornamented.

P_3 elongate, its length approximately equalling that in M_1, subtriangular in basal outline. Longitudinal crest secant, curving lingually moderately abruptly in its posterior extension; crest transected by two or three sets of vertical labial and lingual ridges, these decreasing in strength posteriorly; cuspules produced at crest and these also decrease in strength posteriorly; ridge from anterior cuspid of crest descends anteriorly or slightly anterolingually. Labial and anterior base of crown slightly swollen above roots, but only slightly swollen lingually.

$M_1 < M_2 < M_3 < M_4$; molars subrectangular in basal outline, slightly constricted across talonid

basin; lophids high, moderately convex posteriorly; hypolophid broader than protolophid in M_1, usually broader in M_2 and M_3 but occasionally equal or slightly narrower, and frequently narrower in M_4. Lateral surfaces of lophids nearly parallel, with labial surfaces only very slightly convex and diverging basally. Trigonid basin moderately broad, length almost equalling distance between lophids. Forelink moderately high, strong, descending anterolingually from protoconid then anteriorly across trigonid to near mid-point of moderately high anterior cingulum. Labial moiety of trigonid basin forming relatively deep anterolabial fossette. Slight, variable accessory ridge occasionally present close to and paralleling forelink in lingual moiety of trigonid in anterior molars. Strong, moderately high midlink descends anterolingually from hypoconid, curving anterolabially to unite with slight ridge from point labiad to axis of crown; midlink often puckered near junction. Lingual portion of talonid basin broadly U-shaped, labial portion V-shaped; slight, variable, accessory ridge occasionally present, close to midlink across lingual portion of talonid basin; a slight ridge descends anteriorly from entoconid towards talonid basin. Posterior of hypolophid broadly rounded, occasionally with weak median groove or variable slight ridges.

Cranium of moderate size, elongate. Nasals elongate, subparallel. Maxilla dorsally in moderate contact with frontals; infraorbital foramen opens above anterior root M^1 in specimens with M^4 just erupted. Inferior process of anterior zygoma root moderately developed; post-palatal vacuities large, originating opposite metaloph M^3; palatine extending along lateral margin of vacuity to opposite anterior root M^3. Premaxilla with high to moderately high superior expansions at anterodorsal extremity of mutual suture; anterior palatine foramen originating posteromesial to posterior of I^3, mid-way between this position and premaxilla-maxilla suture. Diastema long. Jugals laterally excavated for insertion of superficial layer of masseter muscle. Lacrymal with lacrymal foramen opening large, at margin of orbit. Remainder of cranium not preserved or too incomplete to be described.

Upper incisors converging anteriorly to form V-shaped series of teeth; I^1 large, axially curved, directed anteroventrally and somewhat mesially, approximated at tips; labial surface curved but lingual surface near planar; facet of wear ascending to I^2. Second upper incisor with short, expanded crown, subrectangular in occlusal view; labial surface with minor groove at posterior one-third. I^3 elongate, spatulate, with well-defined mesial groove. Upper incisors unknown in unworn state.

P^2 and DP^3 unknown.

P^3 elongate, subovate in basal outline, broader posteriorly. Longitudinal crest moderately high, slightly concave labially, transected by two sets of vertical labial and lingual ridges, with the anterior set being better developed; cuspules are produced at crest. Continuations of crest ascend anteriorly from paracone and posteriorly from metacone to unite with ridge curving posterolabially from relatively low hypocone; labial ridge ascending from hypocone unites with lingual ridge from metacone, confining extensive posterolingual fossette; anterior ridge from hypocone ascends to produce sinuous but generally anteriorly convergent lingual cingulum. Cingulum terminates ventrolingual to paracone; low cuspules present along cingulum. Lingual basin broader posteriorly, crossed by continuations of vertical ridges transecting longitudinal crest. Labial base of crown slightly tumid.

$M^1 < M^2 < M^3 < M^4$; molars subrectangular in basal outline, slightly constricted across median valley; lophids relatively high, moderately convex anteriorly, with metaloph broader than protoloph in M^1, approximately equal in M^2, and generally somewhat narrower in M^3 and M^4. Anterior cingulum moderately low, short, relatively broad, descending labially and there united with paracone by well-defined ridge; this ridge generally becomes progressively weaker in posterior molars. Forelink short, variable and occasionally absent, but usually weakly developed from base of protoloph to anterior cingulum above axis of crown. Paracone with slight, variable posterior ridge ascending into median valley. Midlink moderately high, strong, ascending posterolabially from protocone to unite with short ridge from near centre of metaloph; midlink often puckered near junction. Slight ridge from metacone ascends anteriorly into median

TABLE 13: MEASUREMENTS FOR *Macropus (Prionotemnus) agilis siva* (DE VIS)

Specimen	P_3	M_1	M_2	M_3	M_4
F2926*	7·2 × 2·8	—	9·2 × 5·6	10·3 × 6·1	10·9 × 6·3

*Holotype

valley: valley V-shaped in labial and lingual moieties; slight, variable accessory ridge occasionally present close to midlink, in labial part of median valley in anterior molars. Strong posterolabial ridge ascends from hypocone, uniting with weaker ridge ascending posteriorly from metacone at posterolabial base of crown, with production of a posterior fossette; posterolabial ridge from hypocone plicated at fossette.

Discussion: *Macropus (Prionotemnus) agilis* (Gould, 1841) is widespread throughout tropical northern Australia and is also represented in New Guinea. Three geographical subspecies have been recognized within Australia, these being *M. agilis agilis* (Gould) from the northern portion of the Northern Territory, *M. agilis nigrescens*, Lönnberg from the Kimberley area of Western Australia, and *M. agilis jardinei* (De Vis) from the northern and eastern parts of Queensland to about as far south as the Fitzroy River. This subspecies has also been recorded, however, from Stradbroke Island, Moreton Bay, southeastern Queensland, by Longman (1922). Recent work in Moreton Bay suggests that *M. agilis* may be more widespread in that area and may be present on Peel Island as well as on Stradbroke. A single subspecies, *M. agilis papuanus* (Peters and Doria), has been defined in New Guinea.

Distinctions between the recent subspecies have been summarized generally by Schwartz (1910), but are mainly restricted to variations in pellage colouration. He concluded that no cranial characters could be found to enable separation of the various subspecies. Lönnberg (1913), however, compared the crania of *M. agilis nigrescens* and *M. agilis aurescens* (Schwartz), this latter form having been placed subsequently in synonymy with *M. agilis agilis* by Tate (1948). Lönnberg's distinguishing characters relate largely to shape of the maxilla and amount of constriction of the cranium between the orbits and at the anterior of the palate. These areas are not normally preserved in fossils encountered in the Darling Downs deposits and are only poorly illustrated in a single specimen in the material here referred to *M. agilis siva* (De Vis).

Most of the fossil specimens referred to the successional subspecies, *M. agilis siva*, were included by De Vis (1895) within either *Halmaturus siva* De Vis or *Macropus cooperi* (Owen). The holotype of *M. agilis siva*, F2926, measurements for which are presented in Table 13, has been redescribed and refigured in Bartholomai (1966) as '*Halmaturus*' *siva*. De Vis (1895) considered that *H. siva* may be distinguished from *M. cooperi* mainly on the structure of the permanent lower premolars and anterior lower molars. The longitudinal crest in P_3 in the holotype of *M. cooperi* is markedly tricuspidate, this feature being imitated in gross form, but not duplicated, in only a small proportion of the specimens here referred to *M. agilis siva*. Close examination reveals the presence of two major cusps and two or three cuspules along the longitudinal crest in *M. agilis siva*, but evidence of the presence of the cuspules is reduced by occlusion, producing the apparently unilobate P_3 of the holotype.

The other feature considered diagnostic by De Vis (1895) for *H. siva*, was the presence of an accessory ridge in the lingual moiety of the trigonid basin in anterior molars. This was absent in specimens he referred to *M. cooperi*. Presence of this structure was checked in a large sample of *M. agilis jardinei* from the Townsville area, indicating that this feature is present in a small proportion of specimens. It is suggested that presence or absence of this accessory ridge cannot be regarded as of even subspecific value in the fossil population. Extremely poor preservation of the molars in the holotype of *M. cooperi* prohibits close comparison. It is apparent that in *M. cooperi* all molars display the somewhat offset hypolophid typical of the wallaroo rather than kangaroo group. Size differences are not significant between De Vis' (1895) samples and there has been no hesitation in uniting most of his original material.

Table 14 provides a summary of mandibular and maxillary measurements for specimens of *M. agilis siva*. The Coefficients of Variation generally indicate a slightly more variable condition than in *M. agilis jardinei* investigated by Bartholomai (1971). This is the only living subspecies of *M. agilis* for which sufficient material was available for statistical consideration. Values of V exhibited in *M. agilis siva* are consistent with a single fossil population, as suggested by Simpson *et al.* (1960) for a sample drawn from slightly different stratographic levels. Where values for V are particularly low, the probability of inadequate sampling is indicated.

Specimens of *M. agilis siva* are very similar to those of *M. agilis jardinei*, but differ in the position of the anterior palatine foramen, the diastemal length, in the comparatively greater lengths of P_2, DP_3, M^1, M^3 and M^4, and the relatively shorter length of P_3. The anterior palatine foramen is positioned posteromesiad to I^3 and about mid-way between I^3 and the maxilla-premaxilla suture in *M. agilis siva*, but is approximately level with the posterior of I^3 in *M. agilis jardinei*. This feature is present in only two specimens in the referred sample of *M. agilis siva*. Examination of cranial

TABLE 14: SUMMARY OF MAXILLARY AND MANDIBULAR MEASUREMENTS FOR *Macropus (Prionotemnus) agilis siva* (DE VIS)

Character	Maxilla					Mandible				
	n	O.R.	$\bar{X}$	s	V	n	O.R.	$\bar{X}$	s	V
P_2^2 length	—	—	—	—	—	6	7·0– 7·7	7·4	0·307	4·14
max. width	—	—	—	—	—	6	3·1– 3·5	3·3	0·141	4·28
DP_3^3 length	—	—	—	—	—	9	7·2– 8·5	8·0	0·447	5·59
prot. width	—	—	—	—	—	8	4·0– 4·6	4·3	0·200	4·65
P_3^3 length	1	—	10·2	—	—	28	6·9– 9·5	8·2	0·644	7·86
max. width	2	4·9– 5·0	5·0	—	—	25	2·7– 3·8	3·1	0·256	8·25
M_1^1 length	6	8·7– 9·1	8·9	0·173	1·95	35	6·9– 9·3	8·2	0·745	9·09
prot. width	4	6·6– 7·1	6·9	0·216	3·13	32	4·6– 5·8	5·3	0·295	5·57
M_2^2 length	8	9·6–11·1	10·3	0·534	5·19	49	8·4–10·7	9·7	0·620	6·39
prot. width	6	7·5– 8·2	7·9	0·310	3·92	37	5·6– 6·8	6·1	0·334	5·47
M_3^3 length	7	10·9–11·8	11·4	0·355	3·11	55	9·5–12·0	10·9	0·640	5·87
prot. width	7	8·0– 9·0	8·5	0·430	5·06	50	5·9– 7·8	6·7	0·415	6·20
M_4^4 length	4	11·4–12·4	12·0	0·424	3·54	38	10·9–13·3	11·9	0·509	4·28
prot. width	4	8·1– 8·4	8·3	0·365	4·40	46	6·2– 8·0	6·8	0·457	6·73

prot. = protoloph or protolophid.

remains of *M. agilis* in the collections of the Australian Museum, Sydney, suggests that the position of the incisive foramen varies between living subspecies. As suggested by De Vis (1895), the mandibular diastema appears to be slightly longer in *M. agilis siva* at equivalent stages in dental eruption, but this feature was not evaluated statistically.

Table 15 presents a comparison of the samples of *M. agilis siva* and *M. agilis jardinei* by Student's t test. This indicates significance at or approaching the 0·1% level in all dimensions except the length and breadth of P_3. The Coefficient of Difference has been calculated for these comparisons for statistical evaluation of subspecies, as outlined by Mayr *et al.* (1953). Ride (1964) has indicated that values for C.D. should be 1·5 or larger to establish subspecies and this proviso is met only in the lengths of P_2, DP_3, M^1, M^2 and M^4, all of which, however, are represented by small samples. Of these, it is likely that C.D. values for molars are incongruous, as similar results would be expected for lower molars if genuine differences are present.

The log difference diagram, Fig. 4, shows comparison of upper and lower dentitions of *M. agilis siva* and *M. agilis jardinei* based on mean values for the latter sub-species as a standard. This indicates general concordance of dental proportions of the fossil and living subspecies. Simpson (1941) states that such diagrams do not determine affinities directly, but that similarity of proportions is an important factor in determining

TABLE 15: COMPARISON OF SAMPLES OF *M. agilis siva* (DE VIS) AND *M. agilis jardinei* (DE VIS)

Characters	Maxilla			Mandible		
	t	P	C.D.	t	P	C.D.
P_2^2 length	—	—	—	11·56	0·001	2·04
max. width	—	—	—	4·29	0·001	1·11
DP_3^3 length	—	—	—	9·67	0·001	1·73
prot. width	—	—	—	5·08	0·001	0·95
P_3^3 length	—	—	—	0·11	0·5	—
max. width	—	—	—	—	—	—
M_1^1 length	8·30	0·001	2·41	7·89	0·001	0·74
prot. width	4·36	0·001	1·25	7·49	0·001	0·71
M_2^2 length	4·57	0·001	1·36	9·71	0·001	0·80
prot. width	14·24	0·001	1·09	5·85	0·001	0·50
M_3^3 length	8·12	0·001	1·66	10·36	0·001	0·80
prot. width	4·13	0·001	0·75	4·91	0·001	0·39
M_4^4 length	5·90	0·001	1·54	10·80	0·001	1·07
prot. width	9·70	0·001	0·26	2·84	0·01–0·001	0·25

prot. = protoloph or protolophid.

relationships. The suggestion of close affinity between *M. agilis siva* and living forms of *M. agilis* is supplemented by overall cranial morphological similarity with *M. agilis jardinei*.

Mandibular remains of *M. agilis siva* have never been found associated with cranial specimens. Occlusion is good and morphological and proportional similarities of both upper and lower

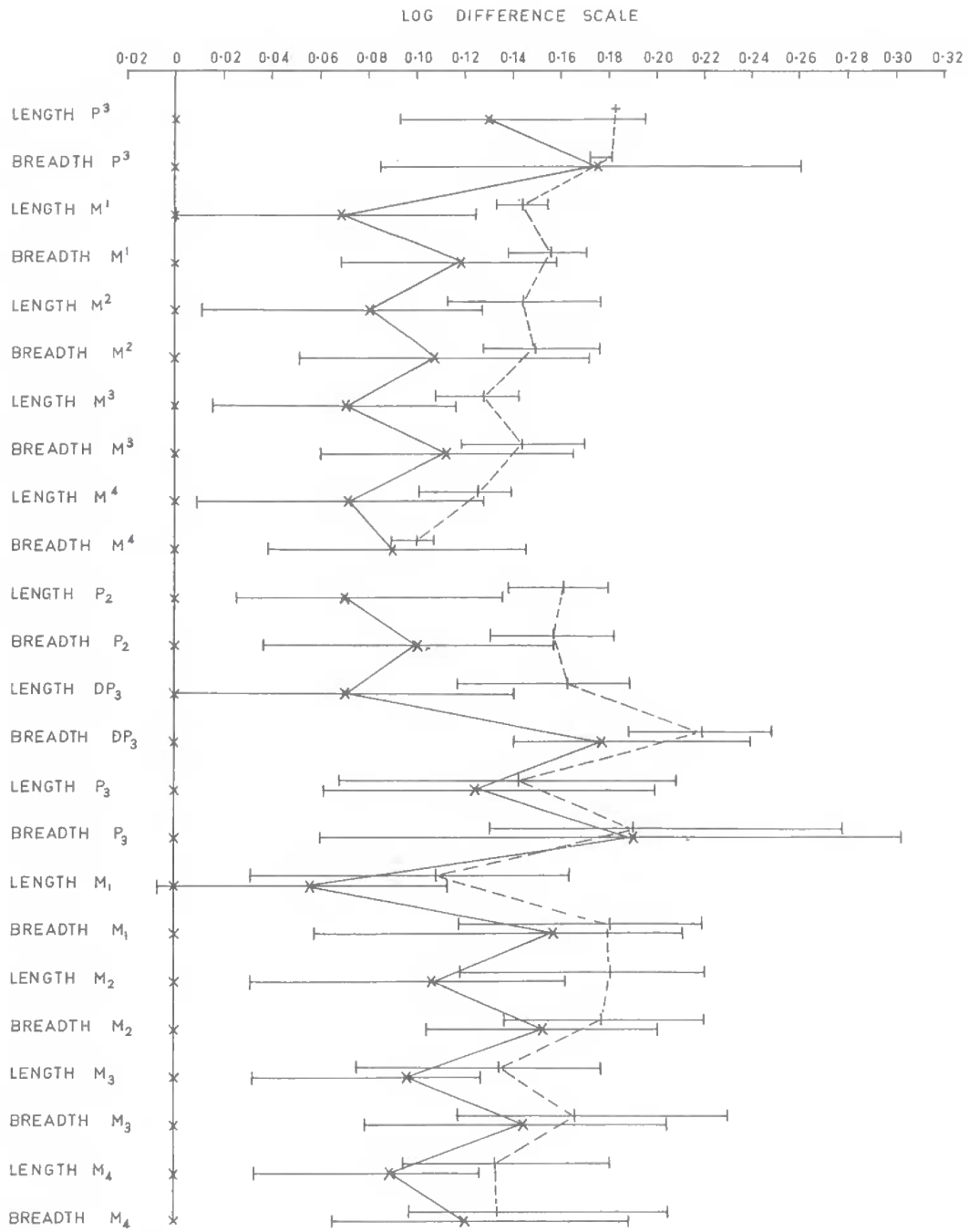


FIG. 4: Log Difference Diagram illustrating proportional relationships of *Macropus (Prionotemnus) agilis siva* (broken line) and *M. agilis jardinei* (solid line) using J4325, *M. dorsalis* as standard. Observed ranges have been included.

dentitions compared with those in *M. agilis jardinei*, indicate their correct association. Maxillary specimens are poorly represented in collections compared with mandibular remains, probably because of the more robust nature of the latter. Post-cranial remains are unknown.

As in the living subspecies, the permanent premolar is erupted before the last molar in both upper and lower dentitions and is reasonably worn by the time the last molar fully erupts.

Progression of the tooth row is moderate, although permanent premolars are retained throughout the life of all individuals encountered.

Material in the Queensland Museum collections indicates the presence of a form either identical with or close to *M. agilis siva* in the late Pliocene Chinchilla Sand. This comprises three mandibular specimens, F3598, F4733 and F4735 and a partial maxilla, F4734. Compared with the sample from the Pleistocene fluviatile deposits, this material is of similar size and, in general, is morphologically identical in the characters preserved. The single juvenile dentition, F3598, differs slightly in having the protolophid of DP_3 reduced to a greater degree than usual, with the lophid crest nearly rectilinear and with the labial portion of the trigonid basin very reduced. A slight ridge flanks the lingual margin of the trigonid, from the metaconid to the anterior cingulum. The posterior ridge from the protoconid is moderately strong. P^3 is more trenchant, being less posterolingually curved than is usual in the Pleistocene sample. The midlink in the molars of this specimen is more direct than normal. It is believed, however, that the variation at present known in the Chinchilla Sand sample could well fall within the limits expected in *M. agilis siva*. On this basis, separation of the Chinchilla sample is not justifiable.

Macropus (?Prionotemnus) gouldi (Owen, 1874)

Osphranter gouldi Owen, 1874, p. 261, pl. 23, figs. 15–6.
Macropus (Osphranter) gouldi Owen, 1877, p. 413, pl. 83, figs. 15–16; Simpson, 1930, p. 72.
Macropus parryi Bennett, 1834; Lydekker, 1887, pp. 220–1.

DISCUSSION: The holotype of the present species was described in very brief form by Owen (1874) and has since been apparently lost. The type locality was not indicated. From the evidence presented in the figures of this specimen (Owen, 1874, pl. 23, figs. 15–16), it is apparent that the specimen is not a juvenile, as suggested by Owen, but presents a fully erupted and ageing cheek tooth row. Lydekker (1887) previously expressed this view, and relegated the species to synonymy with *Macropus (Prionotemnus) parryi*, the living Whiptail Wallaby.

The structure of M_4, the only tooth well preseved in the holotype, is distinct and unlike any other specimens in the collections of the Queensland Museum. Lydekker (1887) suggested that British Museum (Natural History) specimen 43345a, a partial right mandibular ramus, presented by Dr. George Bennett and thus presumably from the fluviatile deposits of the Darling Downs, is indistinguishable from the holotype. M_4 in the holotype presents a much narrower hypolophid than protolophid, indicating its correct assignment in the cheek teeth series.

This tooth is broader across the trigonid basin than is normal in *M. parryi*, and has lower lophids. Its midlink is more direct and appears lower. The shape of the mandibular ramus, particularly the orientation of the symphysis, is in keeping with *Macropus* rather than *Wallabia*, but, on the basis of the morphological differences noted above, Lydekker's (1887) action cannot be supported. Its reference to *Prionotemnus* must remain questionable until more adequate material becomes available.

Thus the species is maintained as a distinct element of the Upper Cainozoic macropodid fauna, but it represents one of the least known taxa.

Macropus (?Prionotemnus) piltonensis sp. nov.
(Plate 23, figs. 3–4)

MATERIAL: F4576, a partial right mandibular ramus with I_1, P_2–DP_3, M_1 broken, P_3 unenamelled and not removed, juvenile, Ravensthorpe, Pilton, eastern Darling Downs, from Pleistocene Fluviatile deposits.

DIAGNOSIS: I_1 with lower margin, straight, and generally broadly rounded in section, but with labial and lingual surfaces meeting in slight ridge; upper enamelled flange broadly rounded to tip, giving rise to moderately blunted tip. P_2 with crest markedly curved lingually in its posterior extension, with slight separation of posteromesial cuspid. DP_3 with well-defined but slight posterior cingulum.

DESCRIPTION: P_3, M_2–M_4 and upper dentition unknown.

I_1 moderately large, deep, ascending at low angle, approximated ventrally at incurved tips, with crown subquadrangular in section becoming slightly less so anteriorly; crown flanged dorsolaterally, but generall broadly rounded ventromesially with lateral and mesial enamelled surfaces meeting in slight ridge; dorsolateral flange broadly

curving anteriorly to tip, producing rather blunt, round tip.

P_2 relatively short, robust, subtriangular in basal outline. Longitudinal crest secant, abruptly curving mesially in its posterior extension; crest subdivided into thirds by strong anterior set of vertical labial and lingual ridges and weak posterior set, with production of cuspules along crest; posterior extension of crest marked posteriorly by prominent vertical groove, giving slight separation of posteromesial cuspid.

DP_3 molariform, subtriangular in basal outline, slightly constricted across talonid basin, with hypolophid much broader than protolophid; crests markedly convex posteriorly. Trigonid basin narrow, moderately well-developed labially, elongate, length being slightly less than distance between lophids. Forelink moderately high, slightly curving anterolingually then anteriorly from protoconid to near mid-point of high anterior cingulum; peaked dorsally at junction; lingual moiety of trigonid basin near planar, labial moiety markedly descending, leading to anterolabial fossette. Slight ridge descends anteriorly from metaconid towards trigonid. Midlink moderately high, curving anterolingually then anteriorly from hypoconid across talonid basin to unite with short ridge from protoconid; slight accessory ridge present across lingual portion of talonid, near lingual limit; moderate ridge descends from entoconid towards talonid. Talonid basin V-shaped. Base of hypolophid with moderately narrow, short, well-defined posterior cingulum.

M_1 known only from anterior moiety; protolophid, trigonid basin and anterior cingulum moderately broad. Protolophid crest only slightly convex posteriorly.

DISCUSSION: The present material represents a form quite distinct from other species described from Pleistocene deposits of the Darling Downs or elsewhere in Australia. Unfortunately, it is represented by only a single mandible.

In the structure of its deciduous dentition it is very similar to *M. agilis siva*. It differs in having the posterior extension of the longitudinal crest of P_2 more sharply inturned. It possesses a well-defined posterior cingulum on DP_3 and in this feature, it differs from material referable without question to *Prionotemnus*. It is not inconceivable that with extreme variation, at least the structure in P_2 could be duplicated in specimens of *M. agilis siva*. However, it is in the structure of I_1 that *M. piltonensis* is chiefly distinguished. If this tooth was taken alone, except for the presence of a slight ventromesial ridge, its generic position would be difficult to reconcile. The blunt tip is particularly interesting, not being duplicated in any other species of *Macropus*.

TABLE 16: MEASUREMENTS OF *Macropus (?Prionotemnus) piltonensis* SP. NOV.

Specimen	P_2	DP_3	P_3	M_1
F4576*	7·1 × 3·5	9·3 × 4·6	—	— × 5·6

*Holotype.

Additional material, both mandibular and maxillary, will need to be located before possible relationships of this species with other fossil and living macropodids can be determined.

Macropus (Prionotemnus) thor (De Vis, 1895)
(Plate 23, figs. 1–2; Plate 24, figs. 1–2)

Halmaturus thor De Vis, 1895, pp. 102–4, pl. 17, fig. 2.
Macropus thor (De Vis): Simpson, 1930, p. 73.
'*Halmaturus*' *thor* De Vis: Bartholomai, 1966, pp. 119–20, pl. 17, figs. 1–3.

MATERIAL: F3602, lectotype, partial right mandibular ramus with M_1–M_3, P_3 exposed from above, M_3 erupting, juvenile, Ravensthorpe, Pilton, Darling Downs, SE.Q., (figd in part, De Vis, 1895, pl. 17, fig. 2; figd Bartholomai, 1966, pl. 17, figs. 1–3).

In addition, one juvenile and 9 adult mandibular rami, together with a partial adult cranium have been referred to *M. thor* from the following localities in the Pleistocene fluviatile deposits of the eastern Darling Downs: Gowrie; Clifton: Ravensthorpe, Pilton; Freestone Creek; and from unspecified localities within the Darling Downs, but with specimens possessing preservation in keeping with the eastern Darling Downs deposits.

DIAGNOSIS: P_3 with longitudinal crest divided by prominent vertical grooves at its anterior third, and with posterior moiety transected by set of weak, vertical ridges with production of cuspule at crest; posterior extension of crest slightly curved mesially. Molars with moderately high links, and with posterior of hypolophid usually marked with near-mesial vertical groove and swollen base; base occasionally partially produced into weak posterior cingulum.

DESCRIPTION: Mandible strong, moderately wide and deep. Symphysis elongate, shallow, with moderately deep geniohyal pit. Diastema elongate, with diastemal crest broadly acute; mental foramen moderately large, oval, near diastemal crest. Ventral margin of ramus angular posterior to symphysis, but often acutely or even broadly rounded; base usually well-rounded posteriorly. Well-defined groove present labially, well below alveolar shelf, from between P_3 and mental foramen to

below anterior of M_2; digastric process slight; lingually, broad, shallow depression opens posteriorly into pterygoid fossa. Post-alveolar shelf moderately long, ascending as slight ridge onto mesial surface of coronoid process, above large mandibular foramen. Masseteric crest raised to below level of bases of molars. Anterior margin of coronoid process inclined at approximately 80° to base of mandible. Bulk of coronoid process, condyle and angle of mandible not preserved.

I_1, P_2 and DP_3 unknown.

P_3 relatively short, subovate in basal outline. Longitudinal crest divided by prominent vertical grooves at its anterior third; posterior portion transected by a slight set of vertical labial and lingual ridges, with production of cuspule at crest. Posteriorly, extension of crest curves slightly lingually. Base of crown slightly swollen.

$M_1 < M_2 < M_3 < M_4$; molars subrectangular, slightly constricted across talonid basin; lophids moderately high, somewhat convex posteriorly; hypolophid slightly broader than protolophid in M_1, occasionally so in M_2, but protolophid usually broader in M_3 and M_4. Trigonid basin moderately broad, but somewhat variable, length almost equalling distance between lophids. Forelink high, strong, descending from protoconid curving anterolingually, then anteriorly to near mid-point of anterior cingulum; cingulum moderately high. Well-defined anterolabial fossette present in labial moiety of trigonid basin; extremely slight ridges descend anteriorly and posteriorly from metaconid towards trigonid and talonid basins, respectively. Mid-link from hypoconid moderately high, curving anterolingually then anteriorly to near midpoint of protolophid. Talonid basin V-shaped with minor, variable, accessory ridges occasionally across lingual moiety in some molars, close to midlink. Very slight anterolabial ridge descends from entoconid towards talonid. Posterior surface of hypolophid curved, usually with shallow, variable, near median, vertical groove near base; base of crown swollen but variable in this feature, occasionally partially produced into weak, posterior cingulum.

Anterior of cranium unknown; cranium large, about 100·0 mm posterior to line between anterior of orbits; inferior process of zygoma root moderately strong; palate posteriorly with large vacuities; palatines apparently moderately developed behind vacuities; jugals laterally excavated for insertion of superficial layer of masseter; zygomatic arches laterally expanded, slightly converging anteriorly; roof of braincase gently arched with weak temporal ridges nearly confluent posteriorly; squamosal and extension of jugal with broad, elongate, slightly convex condyle; postglenoid process of squasmosal moderate; ectotympanic deep, complete dorsally; alisphenoid not inflated with foramen ovale bounded anterolaterally by weak groove.

I^{1-3}, P^2, DP^3, P^3 and M^1 not represented.

$M^2 < M^3 < M^4$; molars subrectangular in basal outline, slightly constricted across median valley, with protoloph approximately as broad as metaloph in M^2 but broader in M^3 and M^4. Lophs moderately low, anteriorly bowed. Anterior cingulum moderately high, broad, relatively elongate mesially; subdued forelink extends from near base of protoloph to anterior cingulum, labiad to axis of crown; well-defined ridge ascends from paracone to labial limit of anterior cingulum while slight ridge ascends posteriorly from paracone; cingulum near planar in labial moiety, but descending to moderate degree in lingual moiety. Midlink moderately high, curving posterolabially from protocone then posteriorly to unite with short ridge from near midpoint of metaloph, above median valley; median valley V-shaped. Strong ridge from hypocone and weaker ridge from metacone ascend posteriorly to unite near base of crown, labiad to axis of crown, with production of fossette.

TABLE 17: MEASUREMENTS FOR *Macropus (Prionotemnus) thor* (DE VIS), MAXILLA

Specimen	M^2	M^3	M^4
F4550 rt.	10·4 × 8·8	12·0 × —	13·4 × 10·0
F4550 lt.	—	12·3 × 9·7	13·2 × 10·0

DISCUSSION: In his original description of *Macropus(Prionotemnus) thor*, De Vis (1895) omitted to nominate a holotype. Bartholomai (1966) selected F3602 as lectotype from De Vis' original series of referred specimens, this being one of the best preserved of the series and the specimen figured (De Vis, 1895, pl. 17, fig. 1).

While the structure of P_3 is regarded as highly variable in macropodines, it can be extremely useful taxonomically, particularly if used in conjunction with other characters. Occasionally it can be used by itself, if no overlap with other taxa occurs. De Vis (1895) placed great importance on the morphology of the permanent lower premolar in distinguishing *M. thor*. Although De Vis was justified in the conclusion that the species is distinct, it is known from too few individuals to be distinguished by premolar structure alone. Referred specimens are somewhat variable in molar structure but this variation is not inconsistent with that observed within better known fossil and recent macropodine populations.

Table 18 presents a summary of mandibular measurements for *M. thor*. The sample is small, this having influenced all values for the Coefficient of Variation. The summary by no means expresses the characteristics of the population, but does provide a guide to the attributes of the species.

Figure 5, a Log Difference Diagram, compares *M. thor* with the standard provided by measurements for living *M. dorsalis*. It also incorporates data from other living wallabies, notably *M. parryi* and *M. rufogriseus*. The figure shows a comparatively greater correspondence in proportions between *M. thor* and *M. parryi* than with other wallabies considered. In molar proportions, some similarity is evident between *M. thor* and *M. rufogriseus* or *M. dorsalis* at this time. However, from an examination of material referable to these species, it is probable that the Log Difference Diagram will not be greatly altered by use of statistical data, especially mean values, for cheek teeth in these species.

Cheek teeth in *M. thor* have more in common with those of *M. parryi* than with other wallabies, and it may be that these species are related. Based on size alone, the differences between these species appear to be much broader than between the fossil *M. agilis siva* and the recent *M. agilis jardinei* discussed above.

The permanent lower premolar in *M. parryi* is of similar proportions to that of *M. thor* and usually

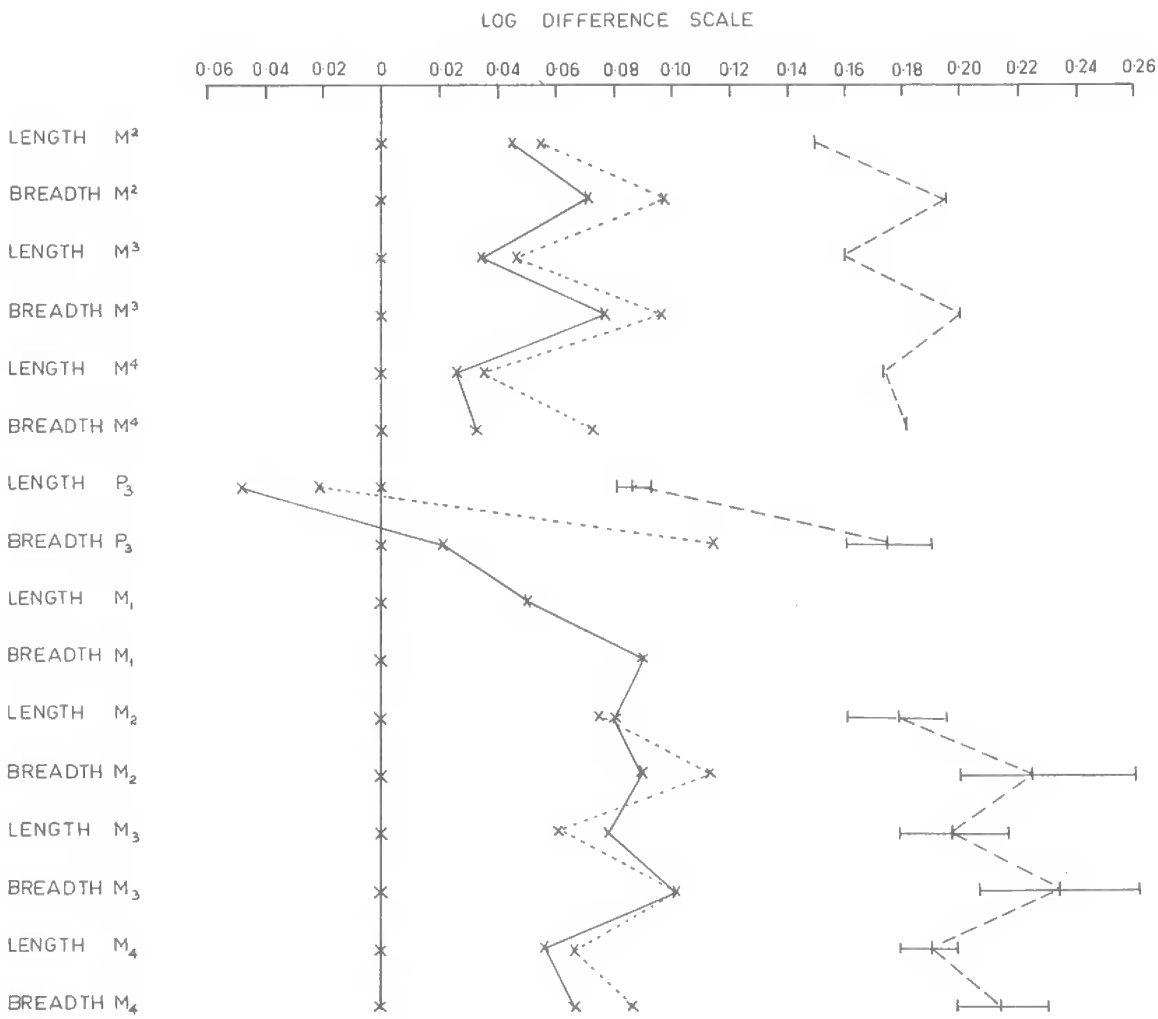


FIG. 5: Log Difference Diagram illustrating proportional relationships of *Macropus (Prionotemnus) thor* (broken line), J10756, *M. parryi* (solid line) and J8128 *M. rufogriseus* (dotted line) using *M. dorsalis* (J4325) as standard. Observed range for *M. thor* has been plotted.

has its longitudinal crest divided by vertical grooves near the anterior cuspid, but has two, or occasionally three, weak sets of ridges transecting the crest posteriorly. Lower molars are basically similar to those in *M. thor*, but the posterior surface, while usually bearing a slight, near median groove, is only very slightly swollen basally, or not swollen at all. Swellings of any kind have not been observed in lower molars in either *M. rufogriseus* or *M. dorsalis*.

TABLE 18: SUMMARY OF MEASUREMENTS FOR *Macropus (Prionotemnus) thor* (DE VIS), MANDIBLE

Character	n	O.R.	$\bar{X}$	s	V
P_3 length	2	7·1– 7·3	7·2	—	—
max. width	2	2·9– 3·1	3·0	—	—
M_1 length	—	—	—	—	—
prot. width	—	—	—	—	—
M_2 length	3	10·0–10·8	10·4	—	—
prot. width	3	6·5– 7·4	6·9	—	—
M_3 length	6	12·1–13·2	12·6	0·438	3·48
prot. width	6	7·4– 8·4	7·9	0·326	4·12
M_4 length	8	13·3–13·9	13·6	0·203	1·50
prot. width	8	7·9– 8·5	8·2	0·207	2·53

prot. = protolophid.

De Vis (1895) did not refer any maxillary specimens to *M. thor*. Measurements for the single cranial specimen here referred are presented in Table 17. These have also been plotted in the Log Difference Diagram (Fig. 5), indicating basic proportional similarity in the characters considered to both *M. parryi* and *M. rufogriseus*, but showing greater similarity to *M. parryi* in the breadth of M^4. As for lower dentition, this is unsupported by statistical data to indicate comparative proportions in tooth dimensions of the populations but is sufficient to support association of the cranial fossil with the mandibular specimens. Occlusion is satisfactory, and morphological comparison with recent specimens shows greater similarity with *M. parryi* than with *M. rufogriseus* or *M. dorsalis*. This is particularly true of the more elongate nature and breadth of the anterior cingulum, development of a weak forelink in most molars, and the possession of large posterior palatine vacuities in *M. parryi*.

Macropus (Prionotemnus) dryas (De Vis, 1895)
(Plate 25, figs. 1–4)

Halmaturus dryas De Vis, 1895, pp. 109–11, pl. 17, figs. 11–15.
Macropus dryas (De Vis): Simpson, 1930, p. 71.
'*Halmaturus*' *dryas* De Vis: Bartholomai, 1966, p. 116, pl. 15, figs. 1–3.

MATERIAL: F3582, lectotype, partial right maxilla with P^3–M^3, adult, ?Chinchilla, SE.Q., ?Chinchilla Sand of Late Pliocene age (figd in part, De Vis, 1895, pl. 17, figs. 13, 15; figd Bartholomai, 1966, pl. 15, figs. 1–3).

Other referred specimens include 2 adult maxillae, an isolated P^3, 17 juvenile mandibular rami, and 39 adult mandibular rami from the following localities in the Chinchilla Sand: Chinchilla; ?Chinchilla; Chinchilla, at M.R.363677 Chinchilla 4-mile map; Chinchilla Rifle Range (Rifle Range No. 78, Par. Chinchilla), in side gully leading into middle gully; and from the western Darling Downs (particular localities unspecified).

DIAGNOSIS: Moderately large species; P^3 elongate, with longitudinal crest nearly straight, and with lingual cingulum low, reduced anteriorly to basal tuberculations; lingual basin narrow. Upper molars with well-defined forelink, lacking strong anterior ridge from paracone. Mandible with labial groove only slightly developed, and with symphysis only slightly elevated to base of mandible. P_2 relatively elongate with posterior extension of longitudinal crest in addition to posterolingual extension. DP_3 with well-defined anterolabial fossette and moderately strong posterior ridge from entoconid to crown base. P_3 elongate, with crown height decreasing somewhat anteriorly; crest nearly straight, only slightly flexed posterolingually. Lower molars high, with moderately low, narrow anterior cingulum and well-defined anterolabial fossette; links high, with accessory ridges occasionally present in lingual moiety of talonid basin; posterior of hypolophid rounded, slightly grooved linguad to crown axis, and with posterior cingulum absent.

DESCRIPTION: Cranium known only from fragmentary maxillary remains.

Upper incisors, P^2 and DP^3 unknown.

P^3 elongate, subtriangular in basal outline, broader posteriorly. Crown with high longitudinal crest, only very slightly concave labially, transected by three sets of vertical labial and lingual ridges,

TABLE 19: MEASUREMENTS FOR LECTOTYPE OF *Macropus thor* (DE VIS)

Specimen	P_3	M_1	M_2	M_3	M_4
F3602	7·1 × 3·1	—	10·4 × —	12·3 × 7·8	—

TABLE 20: MEASUREMENTS FOR *Macropus (Prionotemnus) dryas* (DE VIS), MAXILLA

Specimen	P^3	M^1	M^2	M^3	M^4
F3582*	13·2 × 6·6	9·7 × 8·2	12·1 × 9·3	13·8 × 10·1	—
F3584	—	—	10·7 × 8·8	12·7 × 9·8	—
F3583	14·6 × —	—	— × 9·2	12·1 × 9·5	13·7 × 9·5
F4655	13·8 × 6·7	—	—	—	—

*Lectotype *M. dryas* (De Vis).

with production of cuspules at crest; strength of ridges decreases posteriorly; apex of paracone about one-quarter distance along crown from anterior limit of crown. Hypocone moderately high, being about three-quarters as high as metacone, united to metacone by high, strong, anterolabial ridge; posterior ridge from hypocone curves labially to unite with posterior ridge from metacone, delimiting well-defined posterior fossette; anterior ridge from hypocone ascends towards crown base, with resultant lingual cingulum low, nodular, discontinuous anteriorly, marked by three or four well-defined tubercles, occasionally extending to above paracone. Lingual basin very narrow. Anterolingual crown base swollen, while labial base swollen and nodular.

$M^1 < M^2 < M^3 < M^4$; molars subrectangular, slightly constricted across median valley; lophs moderately high, anteriorly bowed; metaloph broader than protoloph in M^1, but narrower in M^2–M^4. Anterior cingulum relatively low, narrow, moderately short; well-defined strong forelink passes posteriorly from near mid-point of cingulum to centre of protoloph; extremely slight ridge ascends anteriorly from paracone; posterior ridge from paracone into median valley stronger. Midlink high, strong, ascending posterolabially from protocone then posteriorly across median valley to mid-point of metaloph; slight ridge occasionally ascends anterolingually from metacone into median valley; lingual moiety of median valley V-shaped, labial portion sharply U-shaped. Strong posterolabial ridge ascends from hypocone across mid-line of crown, meeting posterolingual ridge from metacone below tooth base, delimiting posterior fossette. Posterior surface of metaloph occasionally ornamented by very slight vertical ridges.

Mandible moderately shallow, relatively thick; base of symphysis elevated slightly to base of mandible; symphysis elongate, shallow, not ankylosed, rugose; geniohyal pit shallow, near posterior symphysial limit; diastema moderately elongate with crest broadly acute, more rounded anteriorly; ventral margin of ramus rounded between symphysis and weak digastric process and ridge. Mental foramen moderate, oval, positioned close to diastemal crest, somewhat anterior to P_3. Ramus with moderately shallow, often ill-defined labial groove extending to below posterior of M_2, about one-third distance from alveolar margin to base of mandible. Digastric process separated from base of angle by shallow post-digastric sulcus, bounded above by shallow digastric fossa; this fossa leads to depression opening posteriorly into pterygoid fossa. Post-alveolar shelf short, leading to post-alveolar ridge, ascending to disappear on mesial wall of coronoid process, above large mandibular foramen. Masseteric crest raised to about level of bases of crowns of cheek teeth; masseteric foramen moderately large, with deep masseteric fossa. Angle of mandible markedly inflected, but bulk of angle, condyle and coronoid process not preserved.

I_1 known only in fractured and worn condition.

P_2 relatively elongate, semi-lunate in occlusal view, with labial surface markedly convex and lingual surface somewhat concave. Longitudinal crest secant, nearly straight, extending posteriorly beyond posterior cuspid, as well as presenting a posterolingual extension; anteriorly, slight lingual curvature evident below anterior cuspid; crest transected by two sets of vertical labial and lingual ridges with production of cuspules at crest; strength of ridges decreases posteriorly. Base of crown somewhat swollen labially.

DP_3 molariform, subtriangular in basal outline, unconstricted across talonid basin, with lophids moderately high, posteriorly convex. Hypolophid much broader than protolophid. Trigonid basin moderately narrow, its length being slightly less than distance between lophids. Forelink high, strong, curving anterolingually from protoconid to point labiad to mid-point of high anterior cingulum; strong ridge descends anteriorly from metaconid across lingual margin of trigonid to unite with anterior cingulum, with production of pocket-like lingual moiety of trigonid; labial moiety reduced, descending rapidly, with well-defined anterolabial fossette present. Midlink moderately high, strong, curving anterolingually from hypoconid across talonid basin to near mid-point of protolophid; moderate ridge descends posteriorly from metaconid into talonid; lingual

moiety of talonid basin sharply U-shaped, labial moiety more broadly U-shaped. Moderate ridge descends posteriorly from entoconid to base of crown, giving posterolingual crown margin an angular appearance. Posterior cingulum not developed.

P_3 elongate, robust, with crown higher posteriorly than anteriorly; suboval in basal outline; longitudinal crest secant, slightly convex labially, slightly curving lingually in its posterior and anterior extensions; crest transected by three sets of vertical labial and lingual ridges with production of cuspules at crest; strength of ridges decreases posteriorly. Anterior cuspid of crest well-defined, posterior cuspid less well-defined. Base of crown swollen labially and lingually.

$M_1 < M_2 < M_3 < M_4$; molars subrectangular in basal outline, slightly constricted across talonid basin; lophids high, convex posteriorly, with hypolophid broader than protolophid in M_1 and M_2 and slightly narrower in M_3 and M_4. Trigonid basin relatively narrow, its length approximately equalling distance between lophids. Forelink high, strong, curving anterolingually from protoconid to near mid-point of moderately high, narrow anterior cingulum; slight ridge descends anteriorly from metaconid towards trigonid basin. Trigonid basin descends labially and lingually from forelink, with anterolabial fossette well-defined. Midlink high, strong, curving anterolingually from hypoconid across talonid basin, to unite with short ridge from near mid-point of protolophid; slight ridge ascends posteriorly from metaconid into talonid, as does slight anterior ridge from entoconid. Talonid basin sharply U-shaped, descending labially and lingually from midlink. Posterior surface of hypolophid generally broadly rounded, usually with poorly defined, broad, vertical groove linguad to axis of crown. Posterior cingulum not developed.

Discussion: Remains of *Macropus (Prionotemnus) dryas* (De Vis) are at present known only from the Chinchilla Sand of late Pliocene age. The lectotype, F3582, was selected from De Vis' (1895) original series of referred specimens and illustrated by Bartholomai (1966).

Reference of the species to the subgenus *Prionotemnus* has been made, although the species differs from others of this group in possessing a well-defined forelink in upper molars and in the presence of some slight grooving on the posterior hypolophid surface in lower molars. In all other preserved features, the species conforms with other members of the subgenus *Prionotemnus*. It is considered that this type of overlap is to be expected in rapidly evolving groups reacting to basically similar evolutionary pressures.

M. dryas is reasonably common in collections from the Chinchilla Sand. It is better represented by mandibular remains than by maxillary. Association of upper and lower jaw fragments has not been observed in the field and reference of mandibular remains is by size and morphological similarity. Occlusion is satisfactory and the present association is considered correct. Post-cranial skeletal elements have not been recorded for *M. dryas*.

The mandibular premolars figured by De Vis (1895, pl. 17, figs. 11–12) are morphologically identical with material here referred to *M. dryas* but it has not been possible to determine the specimen or specimens which formed the subject for these illustrations. Because of the poor illustration, the identity of the M_3 figured by De Vis (1895, pl. 17, fig. 14), is doubtful. The apparent ornamentation of the anterior surface of the protolophid suggests that the specimen may not represent *M. dryas*. De Vis (1895) assigned 73 specimens to *M. dryas*, apparently including some material which is now known to be referable to other species. The only evidence for this is provided by the labels in De Vis' handwriting affixed to individual specimens, but it cannot be confirmed whether these were written at the time of his revision or subsequent to it.

M. dryas is readily distinguished from other Chinchilla Sand species by morphology, but in very worn specimens of this and *Protemnodon chinchillaensis*, the lower molars are difficult to separate. Thus a number of very worn mandibles are doubtfully assigned here, and statistical evaluation of the variation exhibited by the population has been undertaken excluding these specimens.

The summary of mandibular measurements presented in Table 21 indicates Coefficients of Variation similar to those of other fossil macropodids considered in this study. All characters, with the exception of breadth of P_3, show only slight to moderate variation. However, samples of P_2 and DP_3 are inadequate for consideration. As for other species, values are consistent with those from a single species from slightly differing stratigraphic levels (Simpson *et al.*, 1960). The high value for V for breadth of P_3 expresses the relatively more variable nature of this character. Upper tooth parameters, presented in Table 20, are derived from a sample too small for statistical evaluation.

M. dryas represents the most common species of *Macropus (Prionotemnus)* in the Chinchilla Sand. Its relationships with other fossil species are obscure.

TABLE 21: SUMMARY OF MANDIBULAR MEASUREMENTS FOR *Macropus (Prionotemnus) dryas* (DE VIS)

Character	n	O.R.	$\bar{X}$	s	V
P_2 length	3	8·0– 8·9	8·3	—	—
max. width	3	3·4– 3·8	3·6	—	—
DP_3 length	3	8·5– 9·3	9·0	—	—
prot. width	2	4·4– 4·8	4·6	—	—
P_3 length	7	10·2–11·7	11·0	0·5582	5·07
max. width	5	3·6– 4·2	3·9	0·2958	7·58
M_1 length	10	9·7–11·4	10·4	0·5415	5·21
prot. width	9	6·1– 6·9	6·5	0·3724	5·73
M_2 length	19	10·4–12·7	11·6	0·5691	4·91
prot. width	20	7·0– 8·5	7·6	0·3912	5·15
M_3 length	22	11·9–14·0	13·2	0·5515	4·18
prot. width	18	7·1– 9·2	8·3	0·5173	6·23
M_4 length	21	13·8–15·7	14·7	0·6168	4·20
prot. width	23	7·7– 9·6	8·7	0·4953	5·69

prot. = protolophid.

Macropus (Prionotemnus) palankarinnicus Stirton, 1955

(Plate 26, figs. 1–2)

Prionotemnus palankarinnicus Stirton, 1955, pp. 252–8, figs. 3–5.

MATERIAL: F3285, cast of holotype, University of California number 44381, partial right mandibular ramus with P_3–M_4, adult, west side of Lake Palankarinna, east of Lake Eyre, c.29 km S.75°W. of Etadunna Station Homestead (figd Stirton, 1955, fig. 3), of Pliocene age.

F3589, partial right mandibular ramus with P_3–M_4, adult Darling Downs (but preservation indicates derivation from the Chinchilla Sand of late Pliocene age). F6869, very worn right mandibular ramus with P_3–M_4, aged, base of Chinchilla Sand type section, Condamine River, Chinchilla Rifle Range (Rifle Range No. 78, Par. Chinchilla), from the Chinchilla Sand.

DIAGNOSIS: A relatively large species. Mandible with lateral groove descending obliquely and symphysis not greatly downflexed. P_3 relatively elongate with base of crown swollen. Lower molars with comparatively more rectilinear lophids, low links, somewhat convex lateral lophid surfaces, and posterior cingulum.

DESCRIPTION: Mandible relatively large, strong moderately deep; symphysis elongate, elevated at only very low angle to base of mandible, shallow, not ankylosed; geniohyal pit shallow, towards posterior symphysial limit; diastemal crest broadly rounded, except for area immediately anterior to P_3 where crest becomes less rounded. Mental foramen relatively large, oval, set just below diastemal crest, slightly in advance of P_3. Base of mandible broadly rounded posterior to symphysis with extremely weak digastric process; very slight post-digastric sulcus separating process from angle; digastric fossa weak separated above by weak ridge from broad depression opening posteriorly into pterygoid fossa. Moderately weak lateral groove present from P_3 posteriorly to below anterior of M_4, descending from near alveolar margin to slightly above base of mandible. Post-alveolar shelf short, with slight angle, leading to post-alveolar ridge ascending lingual surface of coronoid process. Bulk of angle, process and condyle lacking.

I_1, P_2 and DP_3 not preserved.

P_3 relatively elongate, with longitudinal crest trenchant, transected by three very weak sets of vertical labial and lingual ridges with production of slight cuspules at crest; anterior cuspid well-defined, at slightly higher level than rest of crest; crest posterolingually curved, otherwise approximately straight. Anterior tooth margin very steep. Base of crown labially and lingually swollen, this separated from rest of crown by slight groove; swelling continues around anterior margin.

$M_1 < M_2 < M_3 < M_4$; molars subrectangular in basal outline, slightly constricted across talonid basin in anterior molars, becoming more constricted in posterior molars. Lophids relatively low, nearly rectilinear with slight wear, slightly laterally swollen in anterior view; protolophid slightly narrower than hypolophid in M_1, approximately equal in M_2 and M_3 and broader in M_4. Anterior cingulum relatively low, with trigonid basin broad, moderately elongate, about as long as distance between lophids; cingulum rather squared anterolabially and anterolingually; forelink curves anterolingually from protoconid across trigonid to near mid-point of anterior cingulum; forelink rather low; lingual moiety of trigonid near horizontal, labial portion descends at moderately low angle from forelink. Anterior and posterior ridges from metaconid weak. Midlink descends almost directly from hypoconid across talonid to near mid-point

TABLE 22: MEASUREMENTS FOR *Macropus (Prionotemnus) palankarinnicus* STIRTON, MANDIBLE

Specimen	P_3	M_1	M_2	M_3	M_4
F3285*	9·7 × 4·1	—	10·8 × —	13·3 × —	— × 8·3
F3589	9·5 × 3·7	8·2 × —	9·9 × 7·4	12·5 × 8·2	12·9 × 8·4

*Holotype *M. palankarinnicus* Stirton

of protolophid; midlink rather low. Talonid broadly U-shaped labially and lingually and descends slightly labially and lingually from midlink. Anterior ridge from entoconid weak. Posterior surface of hypolophid with well-defined posterior cingulum.

Upper dentition unknown from Queensland deposits.

DISCUSSION: Although only two specimens referable to this species have been recorded from the Darling Downs area, these are morphologically so similar to the holotype, a cast of which, F3285, is held in the Queensland Museum, that no doubt exists regarding their identification. Stirton (1955) states that the basal swellings on P_3 are not continuous around the anterior margin. However, the holotype cast indicates that this is present, although not as strongly developed as in the Queensland specimen, F3589. P_3 is very slightly longer in the holotype, and other cheek teeth are generally larger. However, compared with the variation exhibited by better known species, these differences are not believed to be significant. The cheek tooth row is straighter in occlusal view in the Queensland specimen than in the holotype.

A second specimen, F6989, with very worn dentition has recently been collected from the Chinchilla Sand. Although less complete than the holotype, reference of this specimen to *M. palankarinnicus* is undertaken with confidence.

Macropus palankarinnicus is the most common macropodid recovered from the Mampuwordu Sands at Lake Palankarinna, in the Tirari Desert of South Australia (Stirton *et al.*, 1961). Stirton (1963) compared it with *Wallabia (sensu lato)* and *Protemnodon* showing its distinctness from the latter. Examination of the extensive sample in the collections of the University of California, Berkeley, was made and while the possibility of a mixed sample exists, it is certain that the material referable to the species is clearly related to the living *Macropus* wallabies.

Ride (1962) suggests that *L. palankarinnicus* does not appear to differ greatly from the Sandy Wallaby, *M. agilis*. However, compared with that species, the molars possess a well-defined posterior cingulum, have more rectilinear lophid crests, lower links and more laterally convex lophid surfaces. The symphysial region of the ramus is not as markedly downflexed.

It is unfortunate that the referred specimen, F3589, is not adequately localised. However, its preservation is wholly consistent with derivation from the Chinchilla Sand of late Pliocene age. This specimen was part of the series referred to *Halmaturus odin* by De Vis (1895), a species regarded as a *nomen dubium* by Bartholomai (1966). It does not present any of the characters considered diagnostic by De Vis (1895) for '*H.*' *odin*.

Measurements for the available sample of *M. palankarinnicus* are presented in Table 22.

DISCUSSION

At present, 12 species of *Macropus* Shaw are recorded from the Upper Cainozoic deposits of Queensland, 8 from the Pleistocene fluviatile deposits and 4 from the late Pliocene Chinchilla Sand. Bartholomai (1972) has drawn attention to the apparent disproportionate number of macropodid species present in the Pleistocene fluviatile deposits of the eastern Darling Downs and this observation is also true of the number of species of *Macropus* represented. It has been suggested by Bartholomai (1972) that this diversity probably reflects, in part, faunal shifts associated with the fluctuating climatic conditions of the Pleistocene. It probably also relates to the assumption that the Pleistocene fluviatile sediments represent approximately similarly aged deposits, whereas this is quite obviously an over-simplification of the temporal relationships within the deposits. However, insufficient information is available to permit more precise resolution of Pleistocene stratigraphy at this time.

Of species of *Macropus* represented in the Tertiary deposits in Queensland, only *M. palankarinnicus* has been recorded elsewhere, having been described from the Pliocene Mampuwordu Sands of the Tirari Desert sequence from central Australia. Restriction of other species to the Chinchilla Sand suggests that these may prove useful in correlation of Tertiary continental deposits.

The origins of *Macropus* are obscure. It is apparent from both morphological and stratigraphic considerations that *Macropus (Macropus)* represents a reasonably recent offshoot from the

earlier developed *M. (Osphranter)* or *M. (Prionotemnus)*. Both these latter subgenera appear to retain features which could have been present in ancestral stock, including better developed, more functional permanent premolars. As in other macropodid genera, there appears to have been a genuine, marked radiation in *Macropus* dating from an origin in the Miocene at the earliest, this regardless of the fact that the late Tertiary and Pleistocene species have been more accessible for collection and study.

LITERATURE CITED

ANDERSON, C., 1929. Palaeontological notes No. 1. *Macropus titan* Owen and *Thylacoleo carnifex* Owen. *Rec. Aust. Mus.* **17:** 35–49.

BARTHOLOMAI, A., 1966. The type specimens of some of De Vis' species of fossil Macropodidae. *Mem. Qd Mus.* **14:** 115–25.

1967. *Troposodon*, a new genus of fossil Macropodinae (Marsupialia). *Mem. Qd Mus.* **15:** 21–33.

1971. Morphology and variation in the cheek teeth in *Macropus giganteus* Shaw and *Macropus agilis* (Gould). *Mem. Qd Mus.* **16:** 1–18.

1972. Aspects of the evolution of the Australian marsupials. Presidential Address. *Proc. R. Soc. Qd* **82:** V–XVIII.

1973a. The genus *Protemnodon* Owen (Marsupialia: Macropodidae) in the Upper Cainozoic deposits of Queensland. *Mem. Qd Mus.* **16:** 309–63.

1973b. *Fissuridon pearsoni*, a new fossil macropodid (Marsupialia) from Queensland. *Mem. Qd Mus.* **16:** 365–8.

CALABY, J. H., 1966. Mammals of the upper Richmond and Clarence Rivers, New South Wales. *C.S.I.R.O. Div. Wildl. Res. Pap.* **10:** 3–55.

1968. Observations of the teeth of marsupials, especially kangaroos. *Dent. Mag. Oral Topics* **85:** 23, 26–7.

CALABY, J. H., MACK, G., and RIDE, W. D. L., 1962. The application of the generic name *Macropus* Shaw, 1790 and of other names commonly referred to the Grey Kangaroo. *Mem. Qd Mus.* **14:** 25–31.

1963. The generic name *Macropus* Shaw, 1790 (Mammalia). Z.N.(S.) 1584. *Bull. zool. Nomencl.* **20** (5): 376–9.

CALABY, J. H., and RIDE, W. D. L., 1964. Notes. *Bull. zool. Nomencl.* **21** (4): 250–5.

DAINTREE, R., 1872. Notes on the geology of the colony of Queensland. *Q.J.G.S.* **28:** 271–358.

DE VIS, C. W., 1889. On a new genus of extinct mammals. *Proc. R. Soc. Qd* **5:** 158–60.

1895. A review of the fossil jaws of the Macropodidae in the Queensland Museum. *Proc. Linn. Soc. N.S.W.* **10:** 75–133.

1899. On some remains of marsupials from Lake Colongulac, Victoria. *Proc. R. Soc. Vic.* (n.s.) **12:** 107–11.

ETHERIDGE, R. JUN. 1878. 'A Catalogue of Australian Fossils.' VIII + 232 pp. (University Press: Cambridge).

1892. Organic remains of the post-Tertiary period. *In* JACK, R. L., and ETHERIDGE, R. JUN., 'The Geology and Palaeontology of Queensland and New Guinea'. *Publ. geol. Surv. Qd* **92:** XVII + 768 pp.

FINLAYSON, H. H., 1964. Notes. *Bull. zool. Nomencl.* **21** (5): 329.

FRITH, H. J., and CALABY, J. H., 1969. 'Kangaroos.' XIII + 209 pp. (F. W. Cheshire: Melbourne).

GLAUERT, L., 1912. Fossil remains from Balladonia in the Eucla Division. *Rec. W. Aust. Mus.* **1:** 47–65.

GOULD, J., 1842. Notes. *Proc. Zool. Soc. Lond.* **1841:** 80–3.

IREDALE, T., and TROUGHTON, E. LE G., 1925. Captain Cook's Kangaroo. *Aust. Zool.* **3:** 311–6.

1934. A check-list of the mammals recorded from Australia. *Mem. Aust. Mus.* **6:** XI + 122 pp.

1937. The identity of Cook's kangaroo. *Rec. Aust. Mus.* **20:** 67–71.

KIRKPATRICK, T. H., 1963. A note on the dental eruption of some Macropodinae, with particular reference to Captain Cook's kangaroo. *Qd J. Agric. Sci.* **20:** 539–41.

1964. Molar progression and macropod age. *Qd J. Agric. Sci.* **21:** 163–5.

1965. Studies of Macropodidae in Queensland: II. Age estimation in the grey kangaroo, the red kangaroo, the eastern wallaroo and the red-necked wallaby, with notes on dental abnormalities. *Qd J. Agric. Anim. Sci.* **22:** 301–17.

KIRSCH, J. A. W., 1968. Prodromus of the comparative serology of Marsupialia. *Nature* **217:** 418–20.

KIRSCH, J. A. W., and POOLE, W. E., 1967. Serological evidence for speciation in the Grey Kangaroo, *Macropus giganteus* Shaw, 1790 (Marsupialia: Macropodidae). *Nature* **215:** 1097–8.

LEMCHE, H., 1964. Notes. *Bull. zool. Nomencl.* **21** (4): 250.

LONGMAN, H. A., 1922. South Queensland marsupials. *Mem. Qd Mus.* **7:** 297–300.

LÖNNBERG, E., 1913. Results of Dr. E. Mjoberg's Swedish scientific expeditions to Australia, 1910–1913; 1, Mammals. *Kungl. Sv. Vetensk. Handl.* **52** (1): 1–10.

LYDEKKER, R., 1887. 'Catalogue of the fossil Mammalia in the British Museum (Natural History)'. Part V. XVI + 345 pp. (Taylor and Francis: London).

MAYR, E., 1964. Notes. *Bull. zool. Nomencl.* **21** (4): 250.

MAYR, E., LINSLEY, E. G., and USINGER, R. L., (1953). 'Methods and Principles of Systematic Zoology.' X + 336 pp. (McGraw-Hill: New York).

MCCOY, F., 1862. Note on the ancient and recent natural history of Victoria. *Ann. Mag. Nat. Hist.* (3) **9:** 137–50.

1867. On the recent zoology and palaeontology of Victoria. *Ann. Mag. Nat. Hist.* (3) **20:** 175–202.

1879. *Procoptodon goliah*. *In* Geological Survey of Victoria. 'Prodromus of the Palaeontology of Victoria', Decade VI, 42 pp. (Govt. Printer: Melbourne).

MORRISON-SCOTT, T. C. S., 1964. Notes. *Bull. zool. Nomencl.* **21** (5): 329.

MORRISON-SCOTT, T. C. S., and SAWYER, F. C., 1950. The identity of Captain Cook's Kangaroo. *Bull. Brit. Mus. (Nat. Hist.) Zool.* **1:** 43–50.

MULLER, P. L. S., 1776. Notes. 'Syst. Nat.' (Linnè) Suppl., p. 62.

OWEN, R., 1838. Fossil Marsupialia from the caves of Wellington Valley. *In* Mitchell's 'Three Expeditions to the Interior of Eastern Australia', Vol. II, pp. 359–63 (T. and W. Boone: London).

(1840-1845).'Odontography.' Vol. I (Marsupials), pp. 373–98.

1845a. Report on the extinct mammals of Australia, with descriptions of certain fossils indicative of the former existence in that continent of large marsupial representatives of the Order Pachydermata. *Rept. Brit. Assoc. Adv. Sci. York* **1844:** 223–40.

1845b. 'Descriptive and illustrative catalogue of the fossil organic remains of mammals and Aves contained in the Museum of the Royal College of Surgeons of England.' IV + 391 pp. (Richard and John E. Taylor: London).

1873a. On the fossil mammals of Australia. Part VIII. Macropodidae: Genera: *Macropus*, *Osphranter*, *Phascolagus*, *Sthenurus*, *Protemnodon*. *Proc. R. Soc. Lond.* **21:** 128.

1873b. On the fossil mammals of Australia. Part IX. Macropodidae: Genera: *Macropus*, *Pachysiagon*, *Leptosiagon*, *Procoptodon* and *Palorchestes*. *Proc. R. Soc. Lond.* **21:** 386–7.

1874a. On the fossil mammals of Australia. Part VIII. Family Macropodidae: Genera: *Macropus*, *Osphranter*, *Phascolagus*, *Sthenurus* and *Protemnodon*. *Phil. Trans.* **164:** 245–87.

1874b. On the fossil mammals of Australia. Part IX. Family Macropodidae: Genera: *Macropus*, *Pachysiagon*, *Leptosiagon*, *Procoptodon* and *Palorchestes*. *Phil. Trans.* **164:** 783–803.

1876. On the fossil mammals of Australia. Part X. Family Macropodidae: Mandibular dentition and parts of the skeleton of *Palorchestes;* additional evidence of *Macropus titan*, *Sthenurus* and *Procoptodon*. *Phil. Trans.* **166:** 197–226.

1877. 'Researches on the Fossil Remains of the Extinct Mammals of Australia with a Notice of the Extinct Marsupials of England., 2 vols. XV + 522 pp. (J. Erxleben: London).

RAVEN, H. C., 1929. Kangaroo. *In* 'Encyclopedia Britannica', 14th Ed. **13:** 254–5.

1939. The identity of Captain Cook's Kangaroo. *J. Mammal.* **20:** 50–7.

RIDE, W. D. L., 1962. On the use of generic names for kangaroos and wallabies (subfamily Macropodinae). *Aust. J. Sci.* **24:** 367–72.

1963. The effect of the suppression by the International Commission on Zoological Nomenclature of Zimmermann 1777 upon the stability of the generic name *Macropus* Shaw, 1790. *J. R. Soc. W. Aust.* **46:** 126–8.

1964. A review of Australian fossil marsupials. *J. R. Soc. W. Aust.* **47:** 97–131.

1970. 'A Guide to the Native Mammals of Australia'. XIV + 249 pp. (Oxford University Press: Melbourne).

SCHWARTZ, E., 1910. On the wallabies usually referred to *Macropus agilis* Gould. *Ann. Mag. Nat. Hist.* (8) **5:** 164–6.

SHARMAN, G. B., 1961. The mitotic chromosomes of marsupials and their bearing on taxonomy and phylogeny. *Aust. J. Zool.* **9:** 38–60.

SHARMAN, G. B., CALABY, J. H., and POOLE, W. E., 1966. Patterns of reproduction in female diprotodont marsupials. *In* ROWLANDS, I. W., Editor, 'Comparative Biology of Reproduction in Mammals.' *Symp. Zool. Soc. Lond.* **15:** 205–32 (Academic Press: London).

SHAW, G., 1790. 'Nat. Miscell.' pl. 33 and text.

1800. 'General Zoology' I, 513 pp. (London).

SIMPSON, G. G., 1930. Post-Mesozoic Marsupialia. Pars 47. 'Fossilium Catalogus, I: Animalia.' 87 pp. (W. Junk: Berlin).

1941. Large Pleistocene felines of North America. *Amer. Mus. Novit.* **1136:** 1–27.

SIMPSON, G. G., ROE, ANNE, and LEWONTIN, R. C., 1960. 'Quantitative Zoology.' Rev. Ed. VII + 440 pp. (Harcourt, Brace and Co.: New York).

STIRTON, R. A., 1955. Late Tertiary marsupials from South Australia. *Rec. S. Aust. Mus.* **11:** 247–68.

1963. A review of the macropodid genus *Protemnodon*. *Bull. Dept. Geol. Uni. Calif.* **44:** 97–162.

STIRTON, R. A., TEDFORD, R. H., and MILLER, A. H., 1961. Cenozoic stratigraphy and vertebrate palaeontology of the Tirari Desert, South Australia. *Rec. S. Aust. Mus.* **14:** 19–61.

TATE, G. H. H., 1948. Studies on the anatomy and phylogeny of the Macropodidae (Marsupialia). Results of the Archbold Expeditions, No. 59. *Bull. Amer. Mus. Nat. Hist.* **91:** 237–351.

TEDFORD, R. H., 1967. The fossil Macropodidae from Lake Menindee, New South Wales. *Bull. Dept. Geol. Uni. Calif.* **64:** 1–156.

THOMPSON, D. W., 1959. 'On Growth and Form.' 2 vols. 1116 pp. (University Press: Cambridge).

TROUGHTON, E. LE G. and MCMICHAEL, D. F., 1964a. Notes. *Bull. zool. Nomencl.* **21** (4): 255–9.

1964b. Notes. *Bull. zool. Nomencl.* **21** (5): 329–31.

WATERHOUSE, G. R., 1846. A Natural History of the Mammalia. I, containing the Order Marsupiata, or pouched animals. 553 pp. (Hippolyte Baillière: London).

WOODS, J. T. and KIRKPATRICK, T. H., 1964. Comments on the proposed stabilization of *Macropus* Shaw, 1790 (Z.N.(S.) 1584). *Bull. zool. Nomencl.* **21** (4): 249–50.

PLATE 7

FIG. 1: *Macropus (Macropus) titan* Owen. Lateral view of partial right adult mandibular ramus, F4193, Ravensthorpe, Pilton, Darling Downs, natural size.

FIG. 2: *Macropus (Macropus) titan* Owen. Stereopair of occlusal view of F4193, natural size.

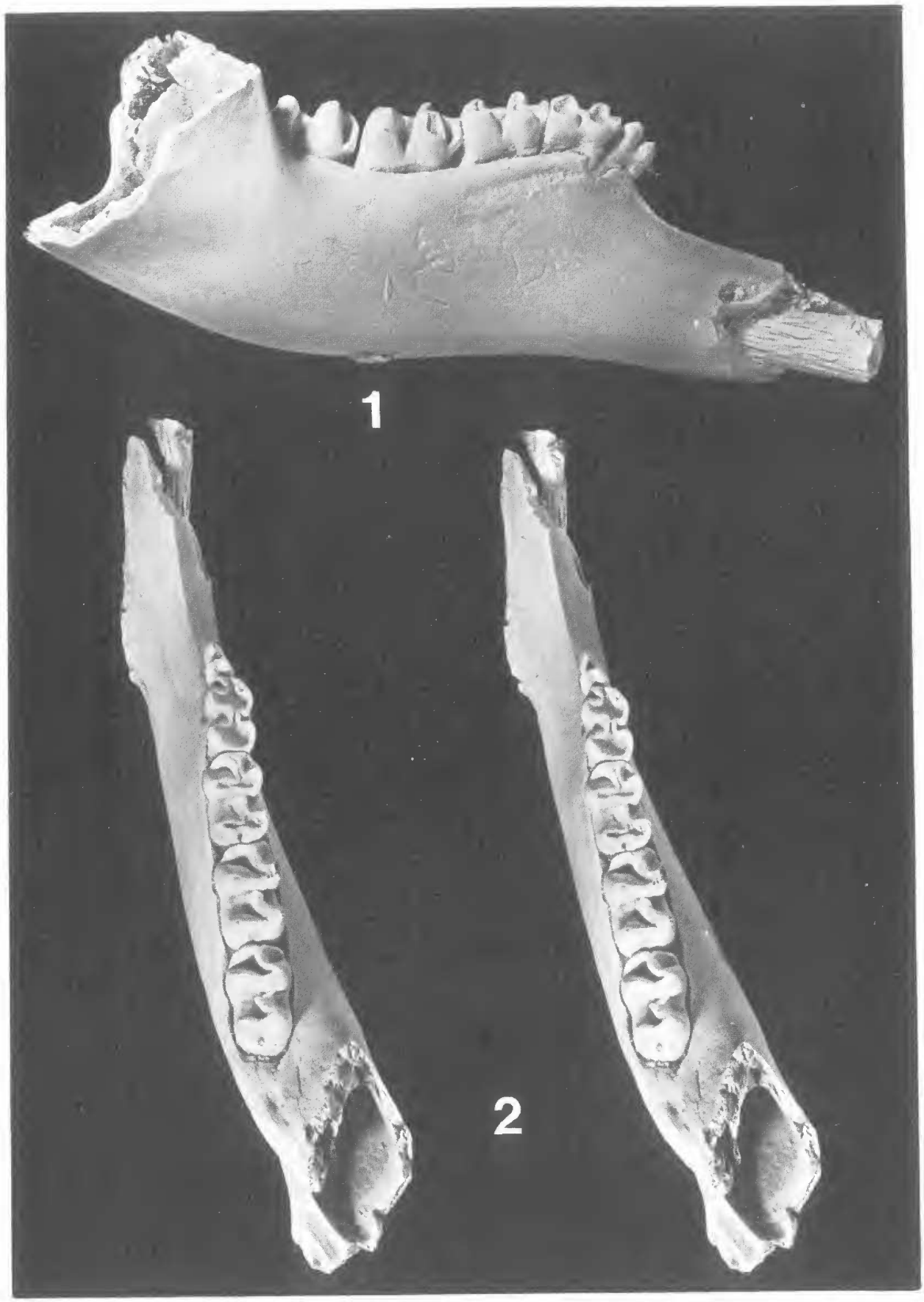

1
2

PLATE 8

FIG. 1: *Macropus (Macropus) titan* Owen. Lateral view of juvenile, partial right mandibular ramus, F3740, Darling Downs, natural size.

FIG. 2: *Macropus Macropus) titan* Owen. Stereopair of occlusal view of F3740, natural size.

FIG. 3: *Macropus (Macropus) titan* Owen. Lateral view of juvenile partial right maxilla, F5716, Dalby, at 30 feet in sewerage drain, Darling Downs, natural size.

FIG. 4: *Macropus (Macropus) titan* Owen. Stereopair of occlusal view of F5716, natural size.

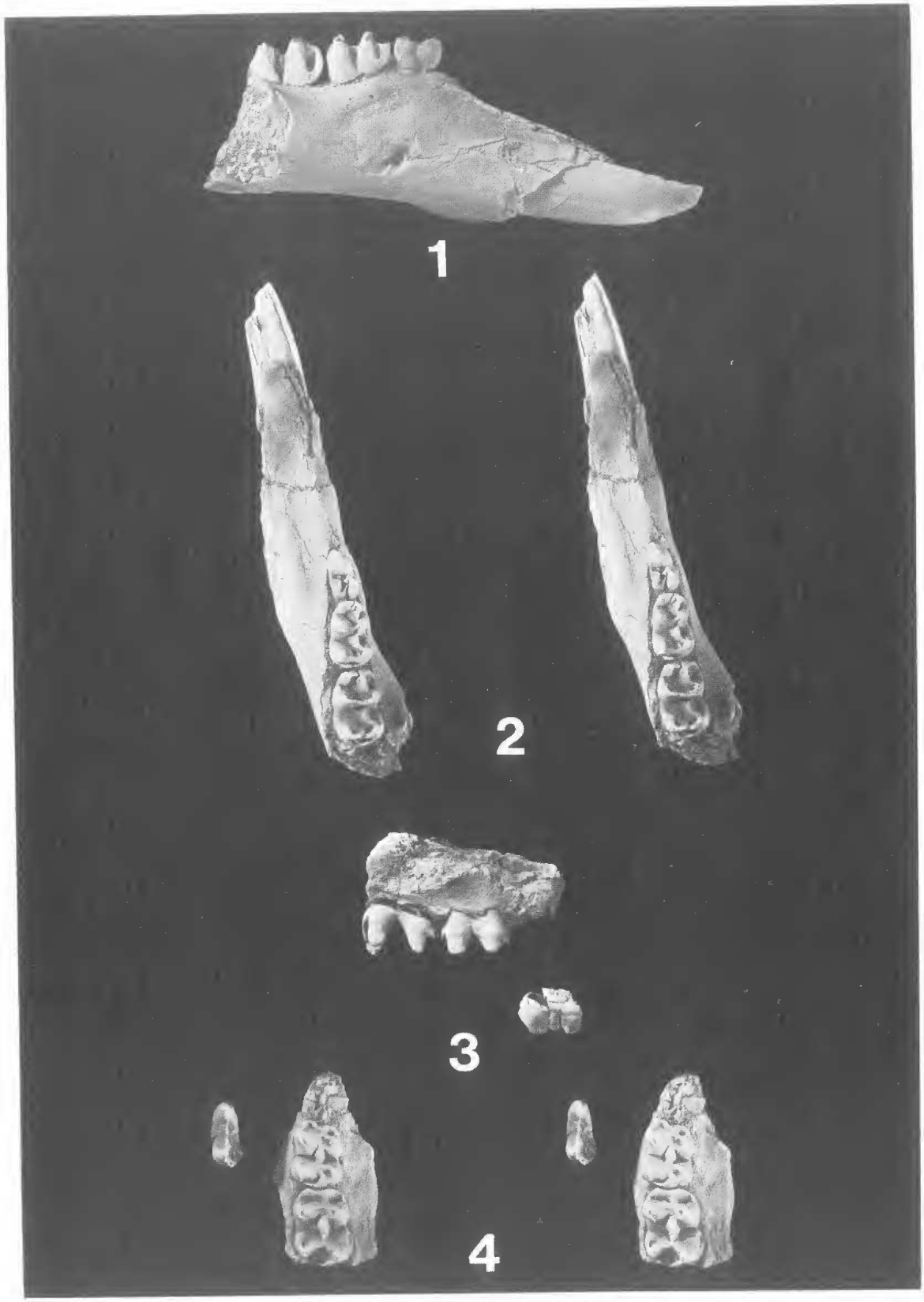

1
2
3
4

PLATE 9

FIG. 1: *Macropus (Macropus) titan* Owen. Lateral view of juvenile partial left maxilla, F4321, Darling Downs, natural size.

FIG. 2: *Macropus (Macropus) titan* Owen. Stereopair of occlusal view of F4321, natural size.

FIG. 3: *Macropus (Macropus) titan* Owen. Lateral view of juvenile partial left maxilla, F3924, Darling Downs, natural size.

FIG. 4: *Macropus (Macropus) titan* Owen. Stereopair of occlusal view of F3924, natural size.

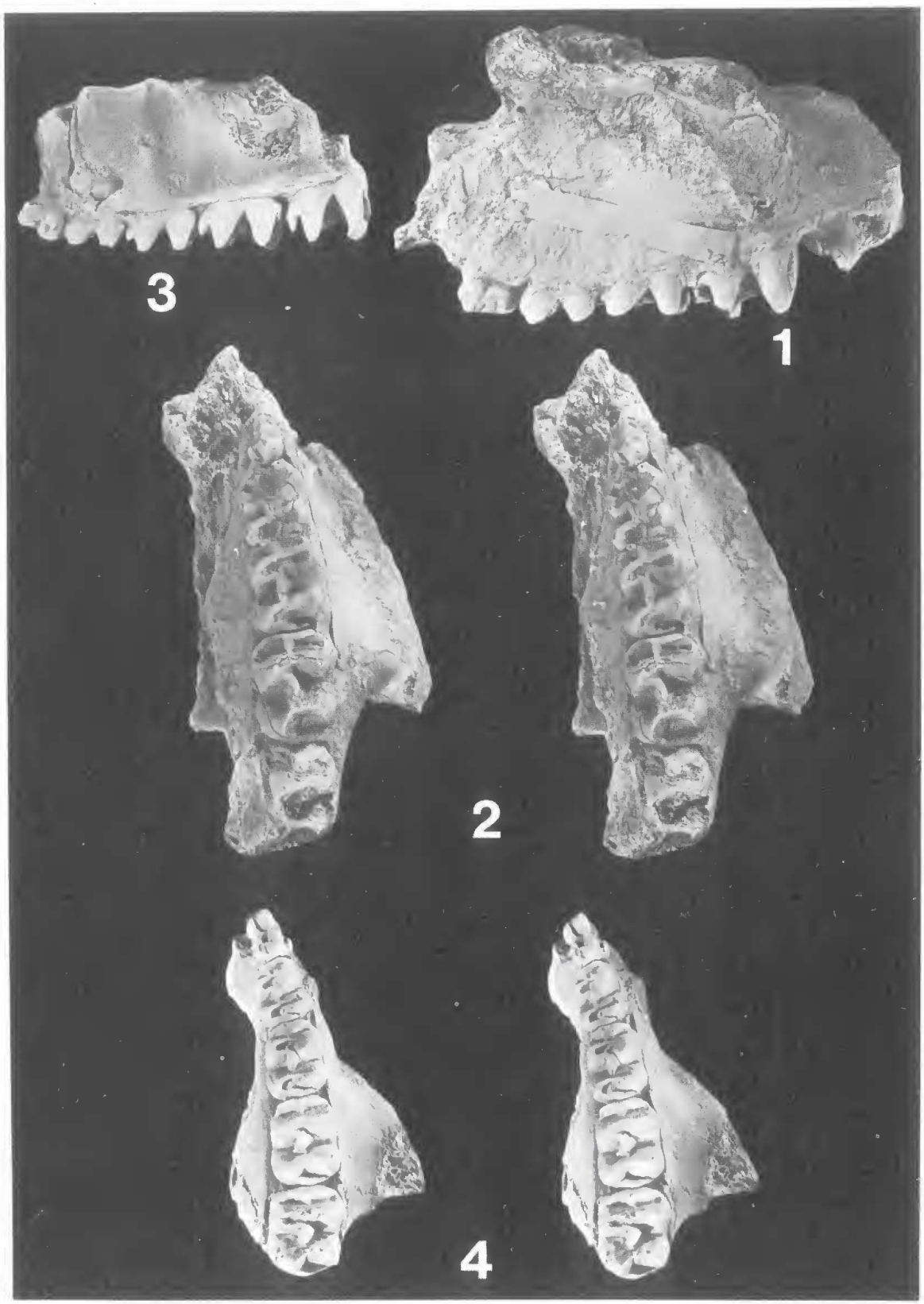

3
1
2
4

PLATE 10

FIG. 1: *Macropus (Macropus) titan* Owen. Lateral view of juvenile left maxilla of partial palate, F4326, Pilton, Darling Downs, natural size.

FIGS. 2, 3: *Macropus (Macropus) titan* Owen. 2, occlusal view of F4326; 3, stereopair of occlusal view of left maxilla of F4326, natural size.

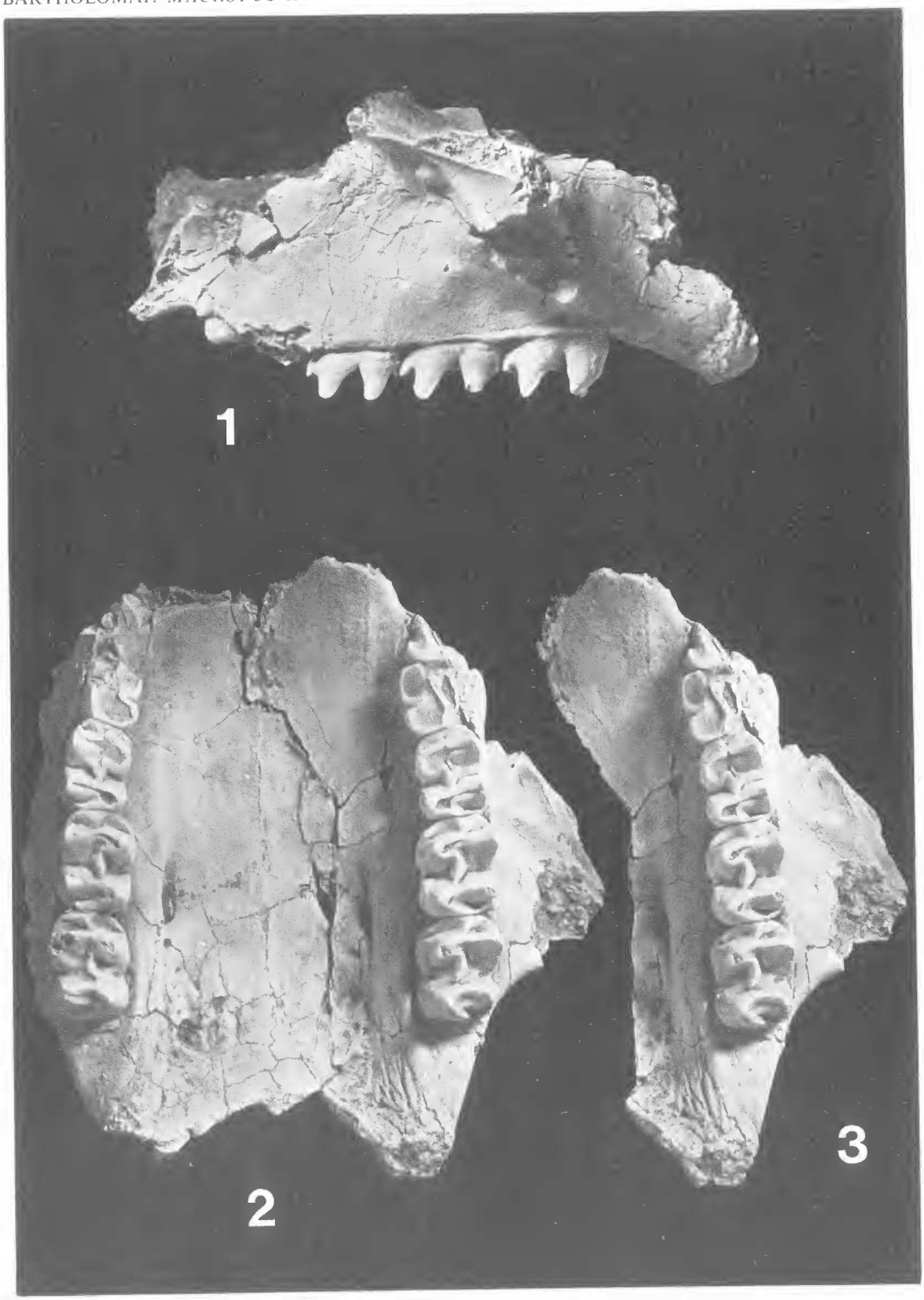

1
2
3

PLATE 11

FIG. 1: *Macropus (Macropus) rama* sp. nov. Lateral view of adult partial left mandibular ramus, F4773, at M.R. 134444 Liverpool Range 1-mile sheet, Pilton, Darling Downs, natural size.

FIG. 2: *Macropus (Macropus) rama* sp. nov. Stereopair of occlusal view of mandible, F4773, natural size.

FIG. 3: *Macropus (Macropus) rama* sp. nov. Lateral view of associated partial right maxilla, F4773, natural size.

FIG. 4: *Macropus (Macropus) rama* sp. nov. Stereopair of occlusal view of maxilla, F4773, natural size.

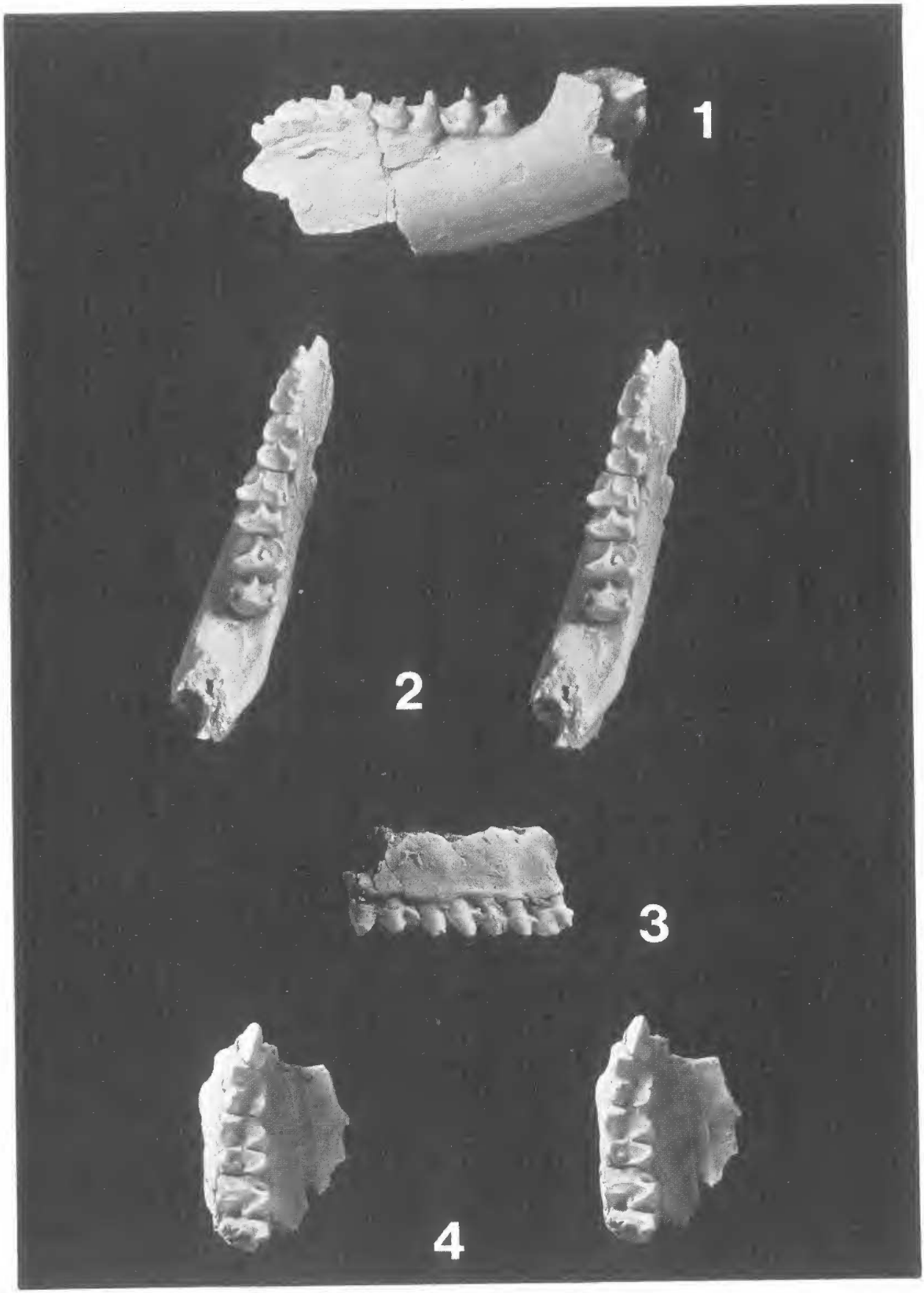

1
2
3
4

PLATE 12

FIG. 1: *Macropus (Osphranter) altus* (Owen). Lateral view of juvenile partial right maxilla, F2849, Bongeen, Darling Downs, natural size.

FIG. 2: *Macropus (Osphranter) altus* (Owen). Stereopair of occlusal view of F2849, natural size.

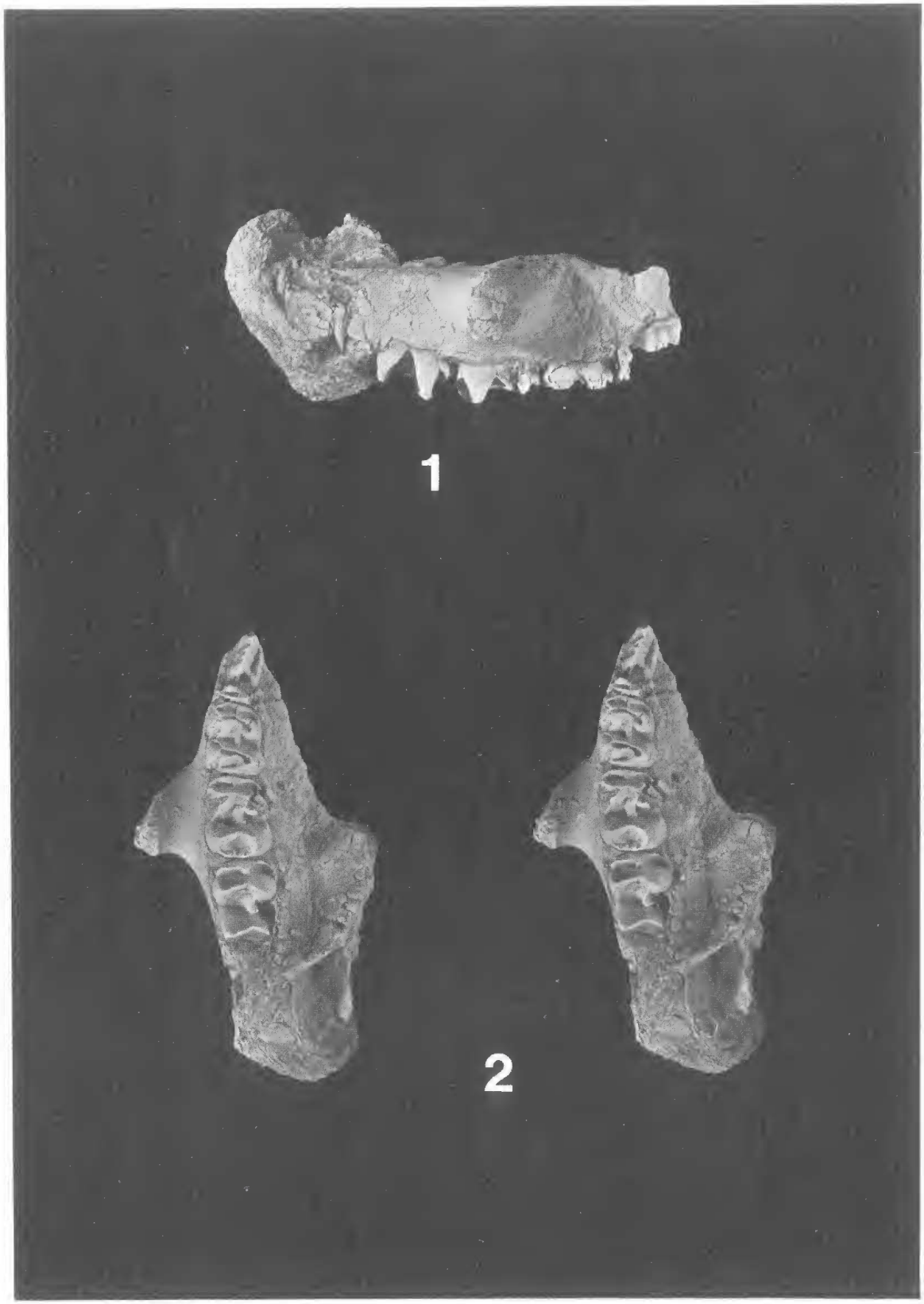

1
2

PLATE 13

FIG. 1: *Macropus (Osphranter) altus* (Owen). Lateral view of adult partial right mandibular ramus, F5441, Darling Downs, natural size.

FIG. 2: *Macropus (Osphranter) altus* (Owen). Stereopair of occlusal view of F5441, natural size.

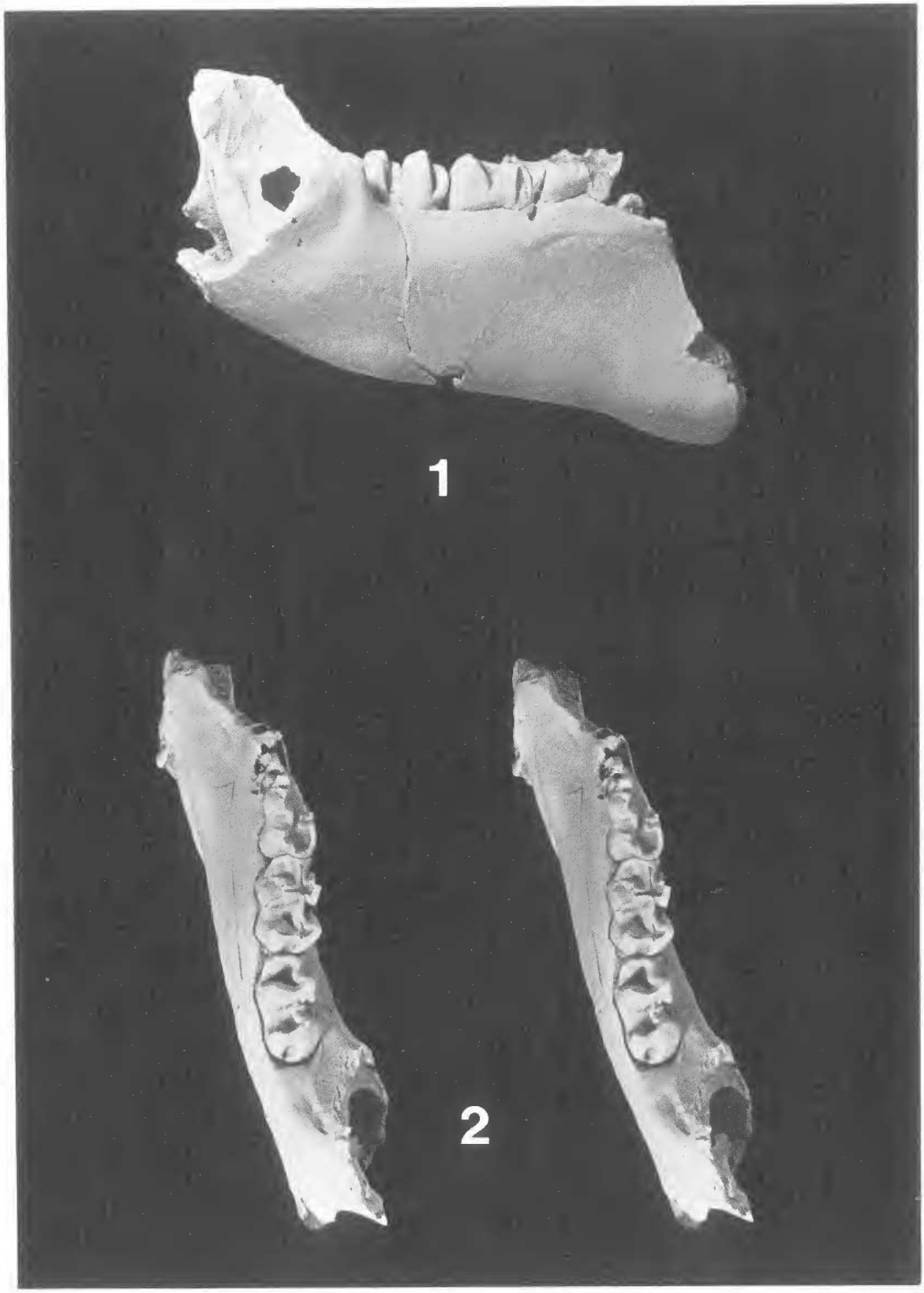

1
2

PLATE 14

FIG. 1: *Macropus (Osphranter) ferragus* Owen. Lateral view of adult partial left maxilla, F3720, Ravensthorpe, Pilton, Darling Downs, natural size.

FIG. 2: *Macropus (Osphranter) ferragus* Owen. Stereopair of occlusal view of F3720, natural size.

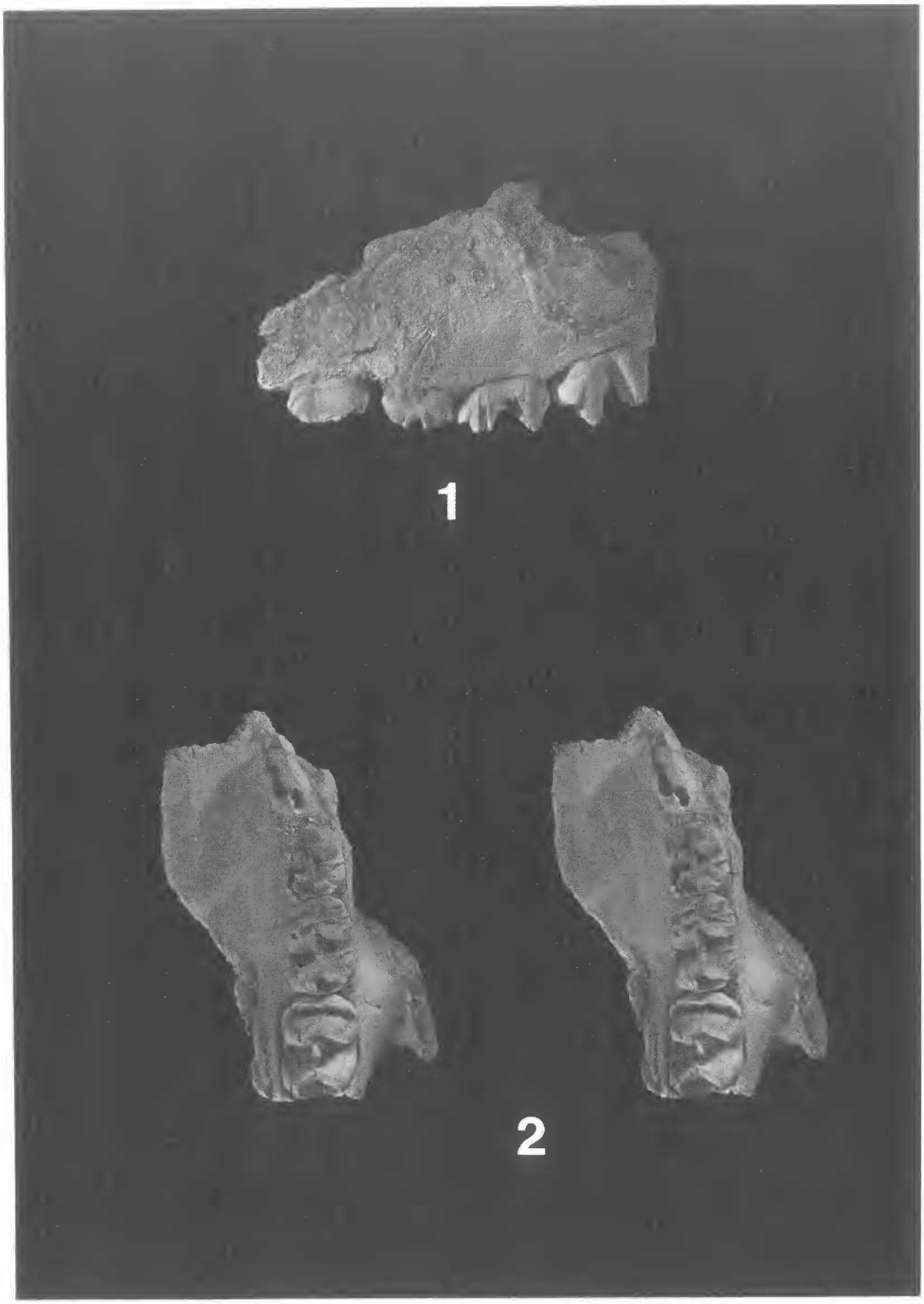

1
2

PLATE 15

FIG. 1: *Macropus (Osphranter) ferragus* Owen. Lateral view of juvenile partial left mandibular ramus, F3974, Darling Downs, natural size.

FIG. 2: *Macropus (Osphranter) ferragus* Owen. Stereopair of occlusal view of F3974, natural size.

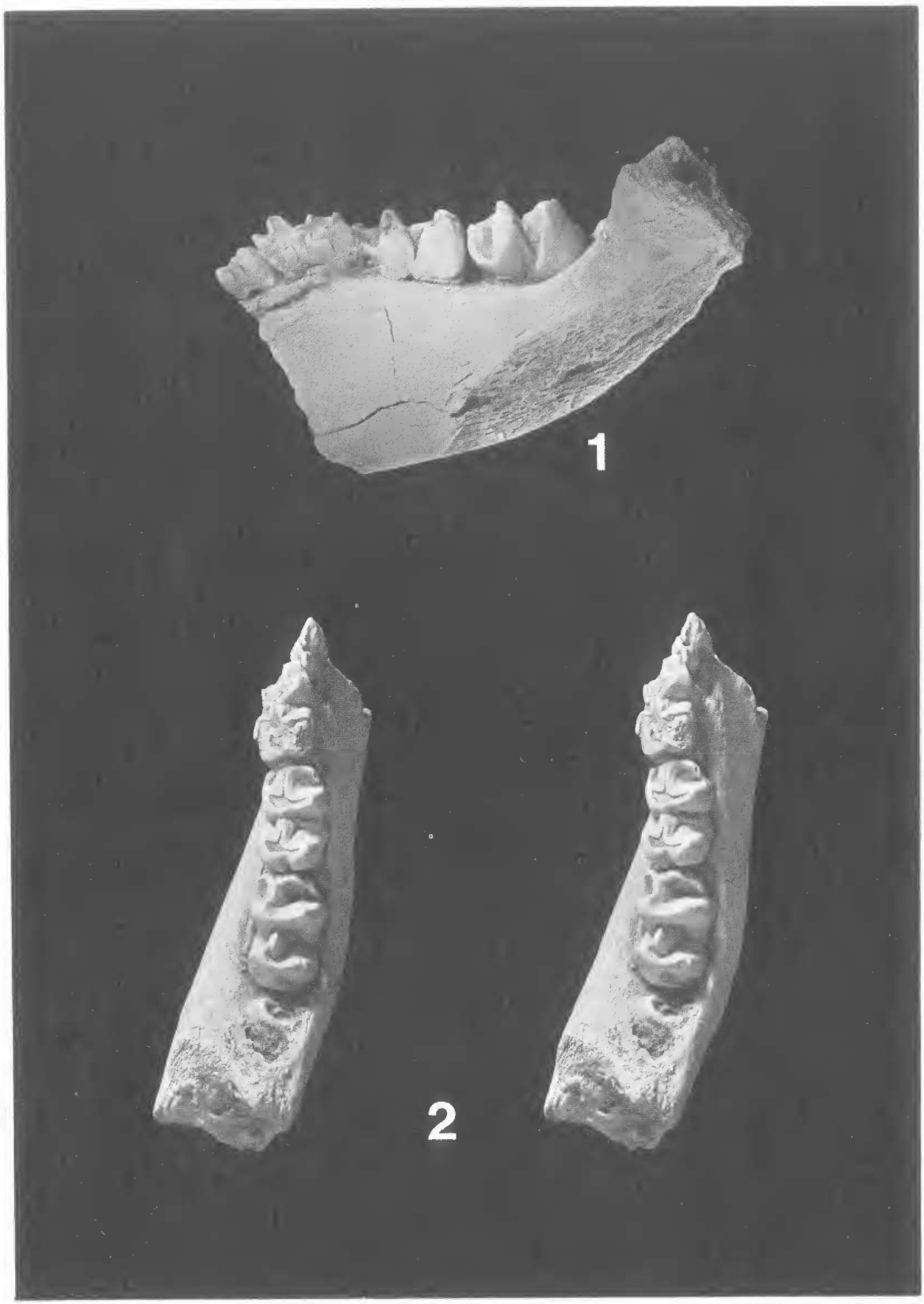

1
2

PLATE 16

FIG. 1: *Macropus (Osphranter) pan* De Vis. Lateral view of adult partial left maxilla, F3713, Chinchilla, Darling Downs, natural size.

FIG. 2: *Macropus (Osphranter) pan* De Vis. Stereopair of occlusal view of F3713, natural size.

FIG. 3: *Macropus (osphranter) pan* De Vis. Lateral view of adult partial right maxilla, F3714, Chinchilla, Darling Downs, natural size.

FIG. 4: *Macropus (Osphranter) pan* De Vis. Stereopair of occlusal view of F3714, natural size.

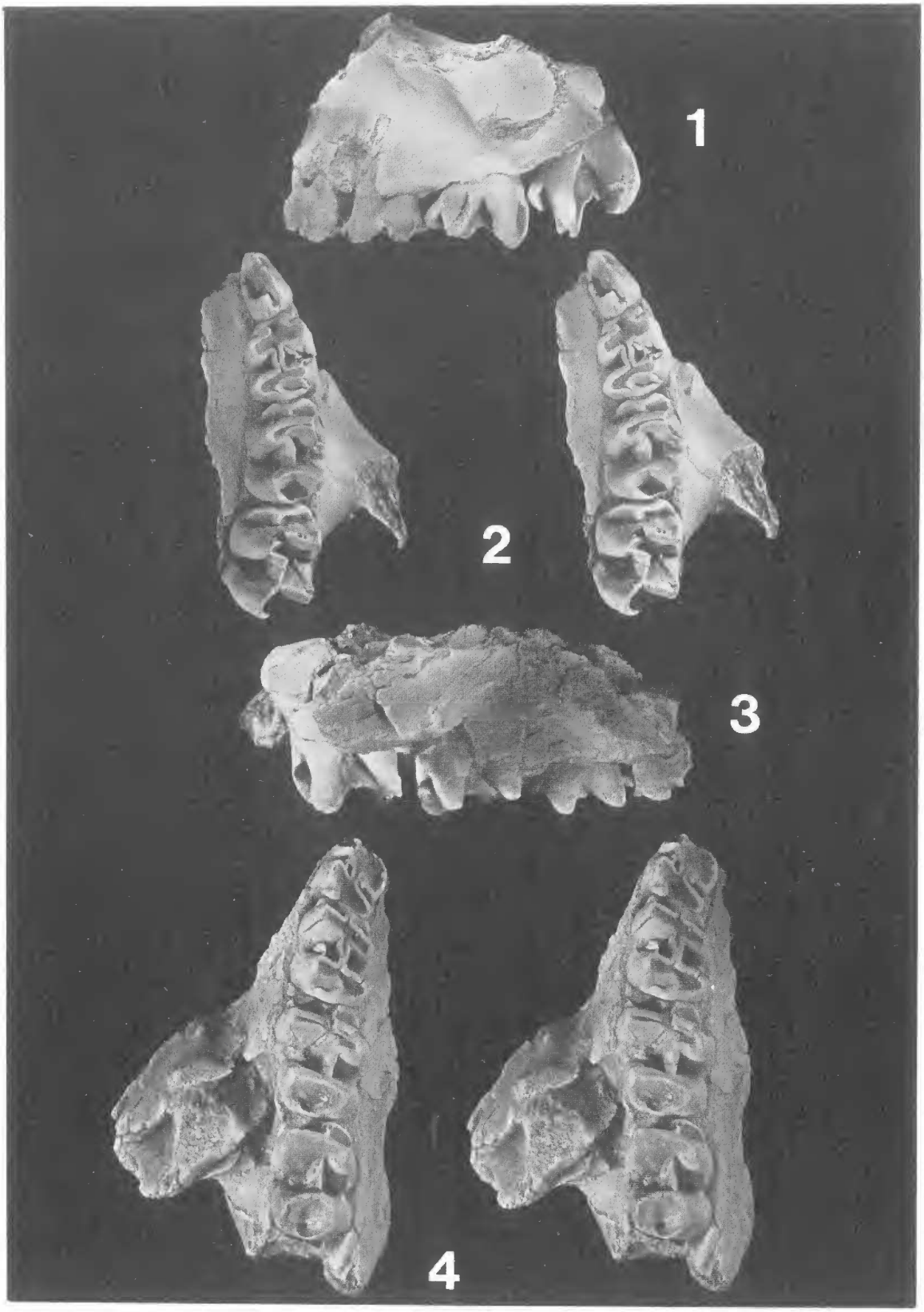

1
2
3
4

PLATE 17

FIG. 1: *Macropus (Osphranter) pan* De Vis. Lateral view of adult partial left mandibular ramus, F3715, Chinchilla, Darling Downs, natural size.

FIG. 2: *Macropus (Osphranter) pan* De Vis. Stereopair of occlusal view of F3715, natural size.

FIG. 3: *Macropus (Osphranter) pan* De Vis. Lateral view of juvenile partial left mandibular ramus with P_3 removed by fenestration, F3717, Condamine River, near top of bank, 60 metres east of eastern boundary of Chinchilla Rifle Range (Rifle Range No. 78, Par. Chinchilla), Darling Downs, natural size.

FIG. 4: *Macropus (Osphranter) pan* De Vis. Stereopair of occlusal view of F3717, natural size.

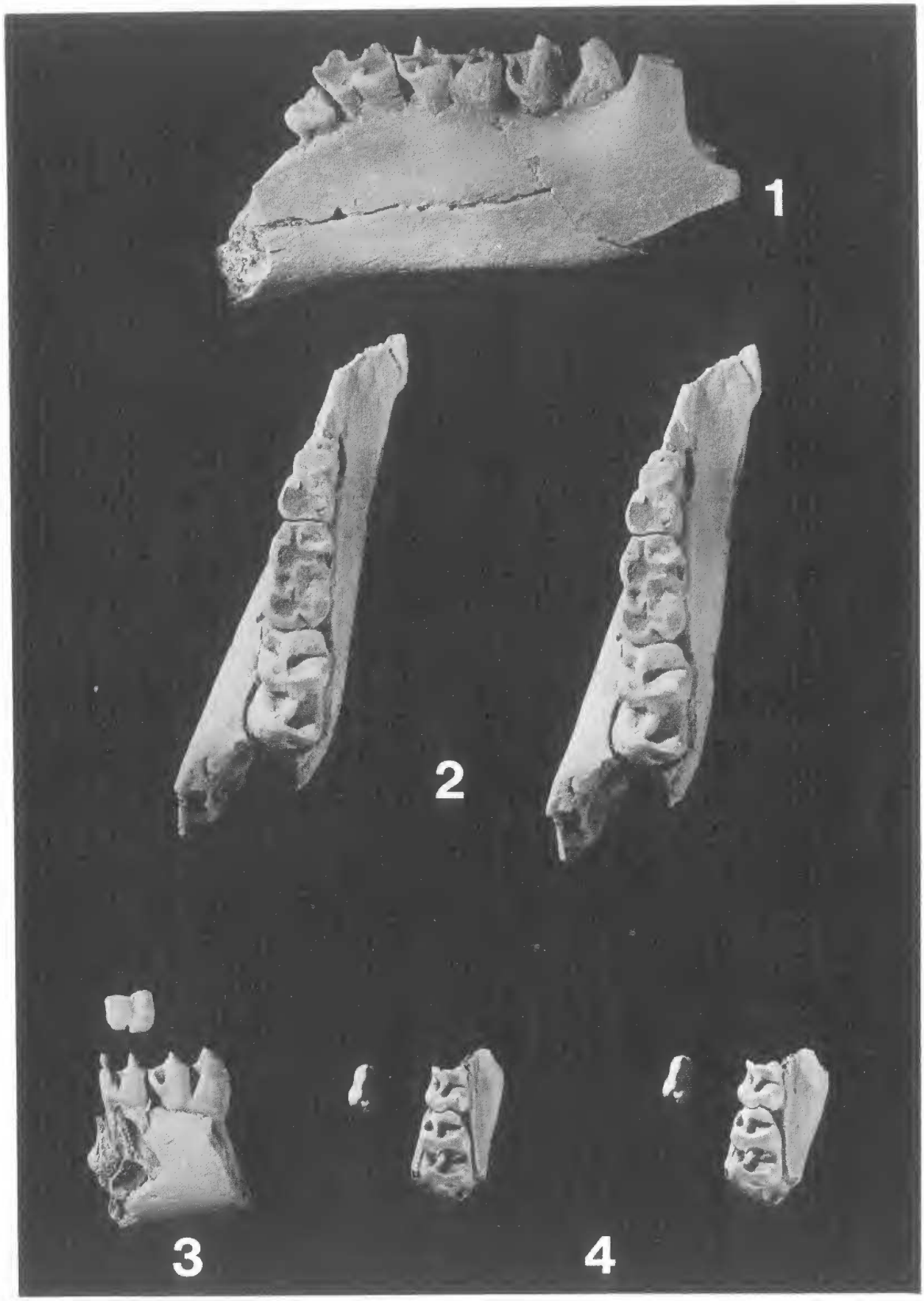

1
2
3
4

PLATE 18

FIG. 1: *Macropus (Osphranter) pan* De Vis. Lateral view of adult partial left mandibular ramus, F3611, western Darling Downs, natural size.

FIG. 2: *Macropus (Osphranter) pan* De Vis. Stereopair of occlusal view of F3611, natural size.


1
2

PLATE 19

FIG. 1: *Macropus (Osphranter) woodsi* sp. nov. Lateral view of holotype, juvenile partial mandibular ramus, F3920, Condamine River end of middle gully system, Chinchilla Rifle Range (Rifle Range No. 78, Par. Chinchilla), Darling Downs, natural size.

FIG. 2: *Macropus (Osphranter) woodsi* sp. nov. Stereopair of occlusal view of F3920, natural size.

FIG. 3: *Macropus (Osphranter) woodsi* sp. nov. Lateral view of adult partial right mandibular ramus, F5460, Chinchilla, Darling Downs, natural size.

FIG. 4: *Macropus (Osphranter) woodsi* sp. nov. Stereopair of occlusal view of F5460, natural size.

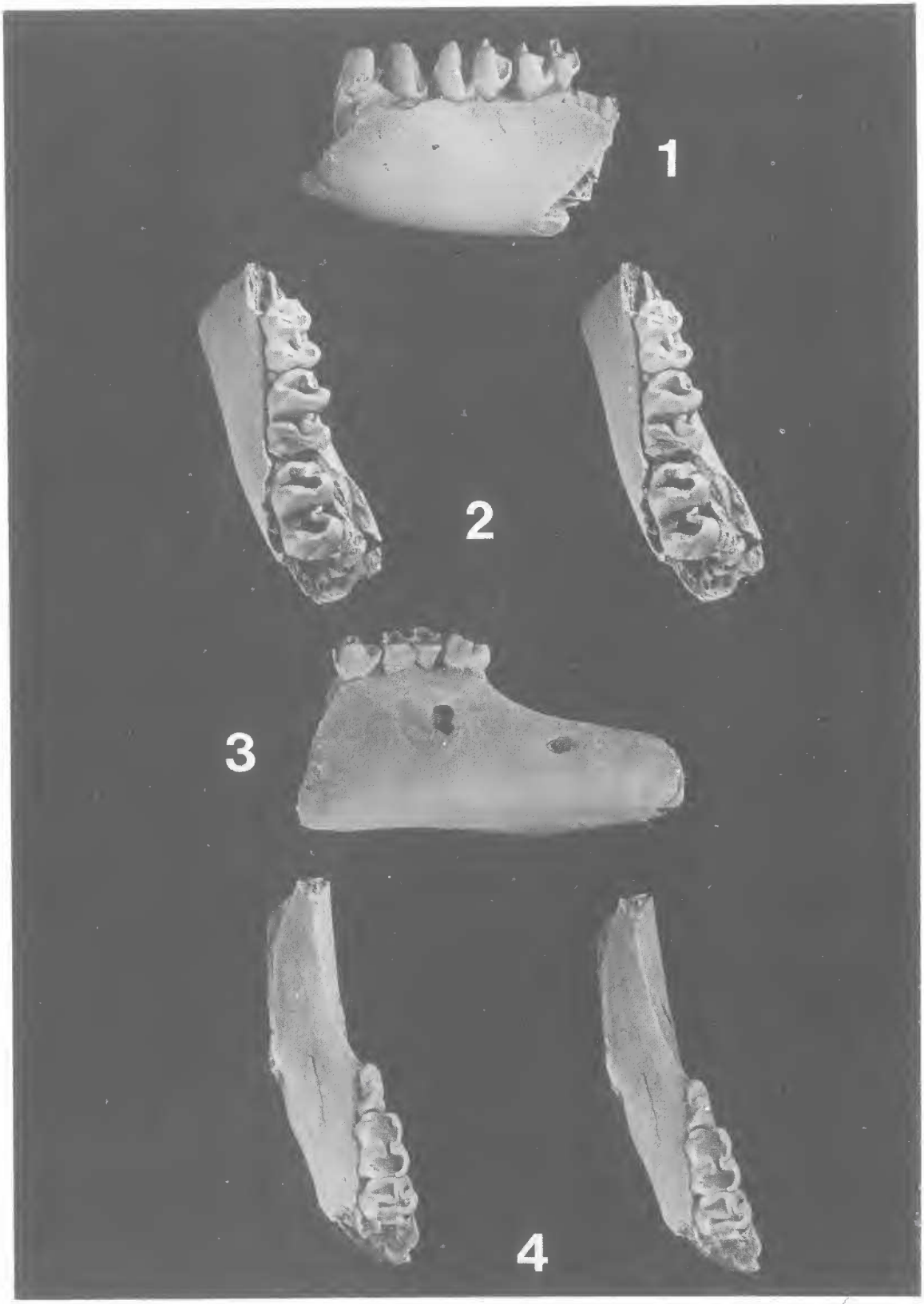

1
2
3
4

PLATE 20

FIG. 1: *Macropus (Osphranter) woodsi* sp. nov. Lateral view of adult partial right mandibular ramus, F40, Warra, Darling Downs, natural size.

FIG. 2: *Macropus (Osphranter) woodsi* sp. nov. Stereopair of occlusal view of F40, natural size.

FIG. 3: *Macropus (Osphranter) woodsi* sp. nov. Lateral view of adult partial right maxilla, F3718, western Darling Downs, natural size.

FIG. 4: *Macropus (Osphranter) woodsi* sp. nov. Stereopair of occlusal view of F3718, natural size.

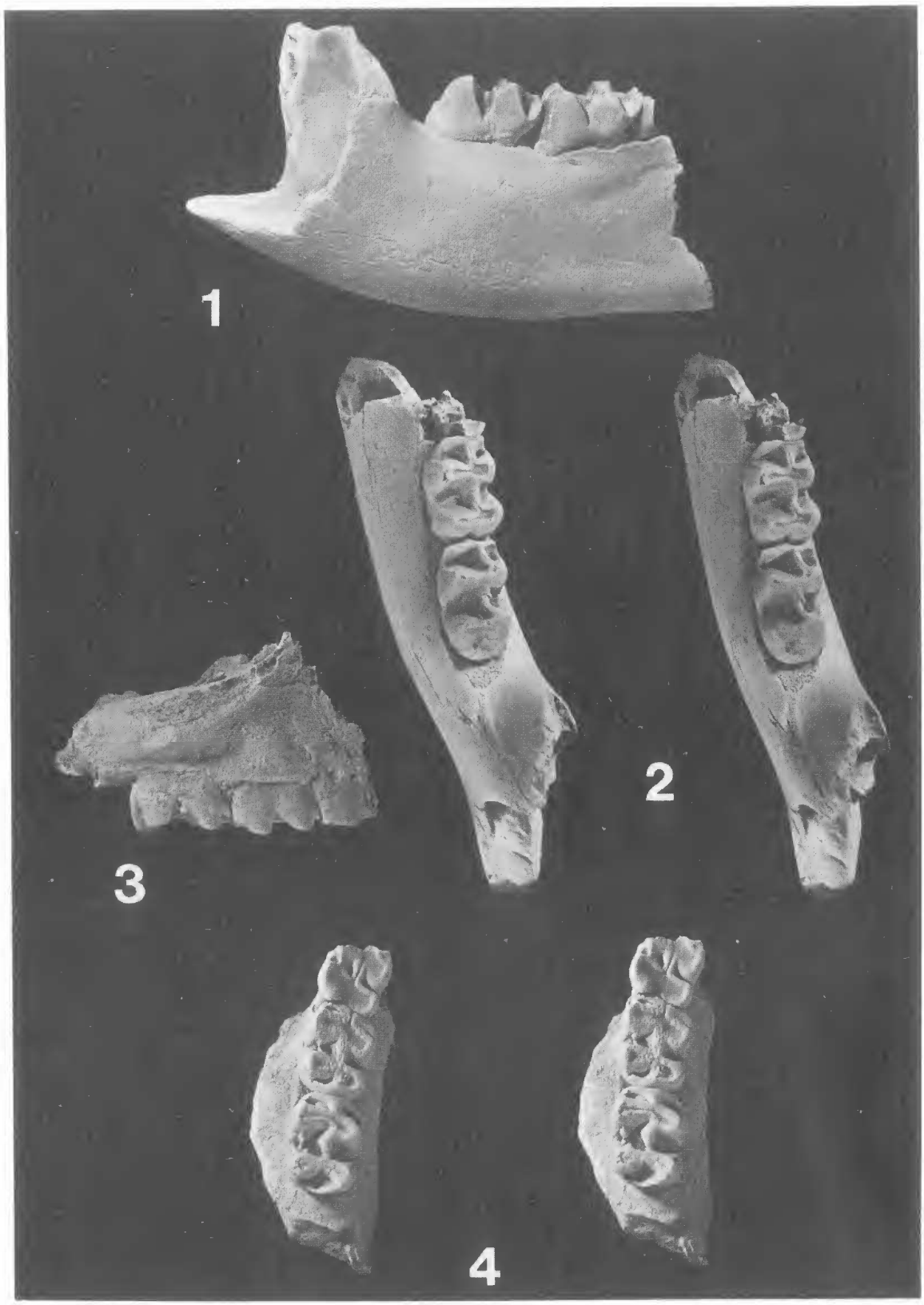

1
2
3
4

PLATE 21

FIG 1: *Macropus (Prionotemnus) agilis siva* (De Vis). Lateral view of adult partial left mandibular ramus, F4492, Gowrie, Darling Downs, natural size.

FIG. 2: *Macropus (Prionotemnus) agilis siva* (De Vis). Stereopair of occlusal view of F4492, natural size.

FIG. 3: *Macropus (Prionotemnus) agilis siva* (De Vis). Lateral view of juvenile partial right mandibular ramus with P_3 removed by fenestration, F4483, ?Gowrie, Darling Downs, natural size.

FIG. 4: *Macropus (Prionotemnus) agilis siva* (De Vis). Stereopair of occlusal view of F4483, natural size.

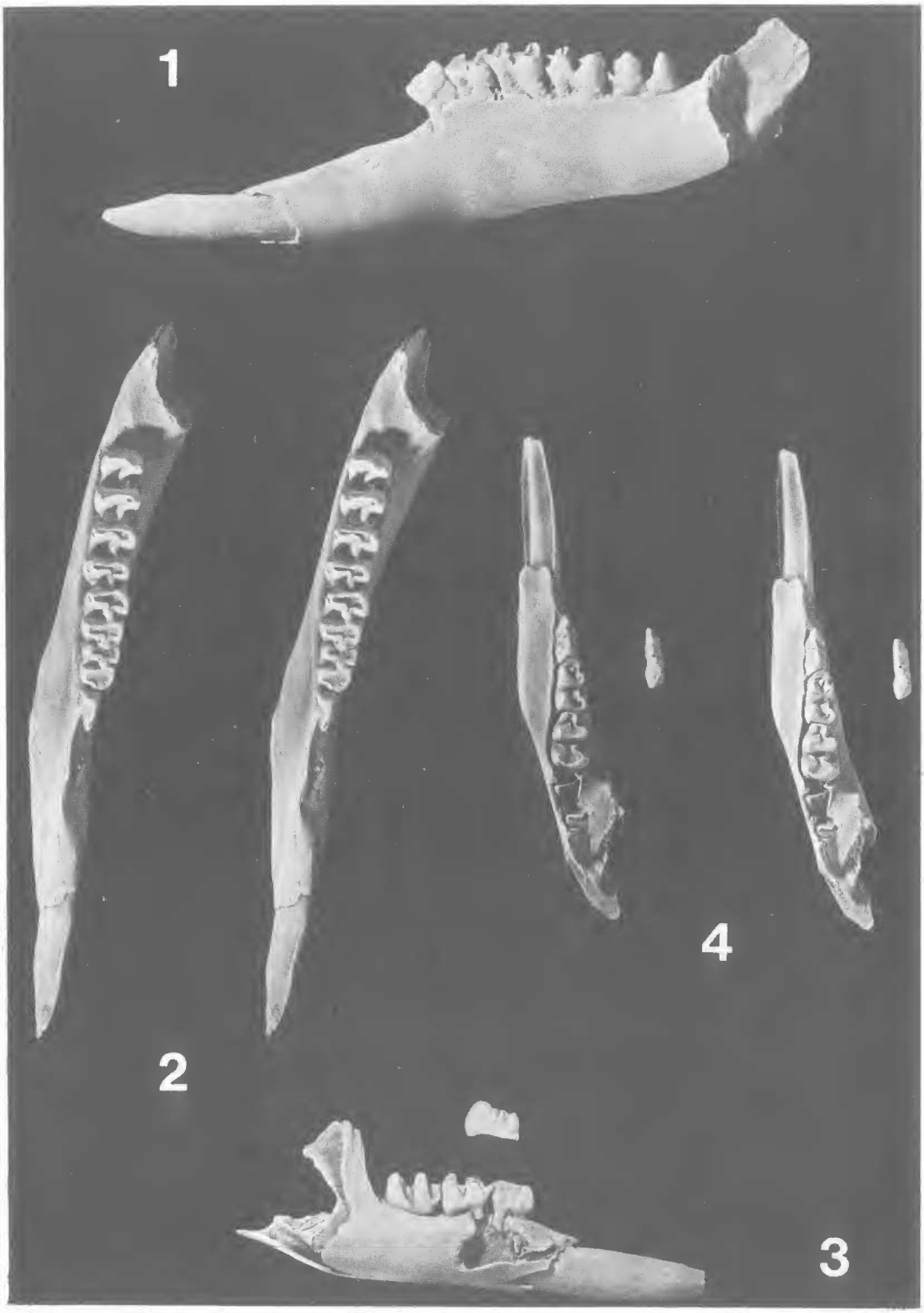

1
2
3
4

PLATE 22

FIG. 1: *Macropus (Prionotemnus) agilis siva* (De Vis). Lateral view of adult partial cranium, F652, Gowrie, Darling Downs, natural size.

FIG. 2: *Macropus (Prionotemnus) agilis siva* (De Vis). Stereopair of occlusal view of F652, natural size.

FIG. 3: *Macropus (Prionotemnus) agilis siva* (De Vis). Stereopair of occlusal view of juvenile partial left maxilla with P^3 exposed by fenestration, F4541, Darling Downs, natural size.

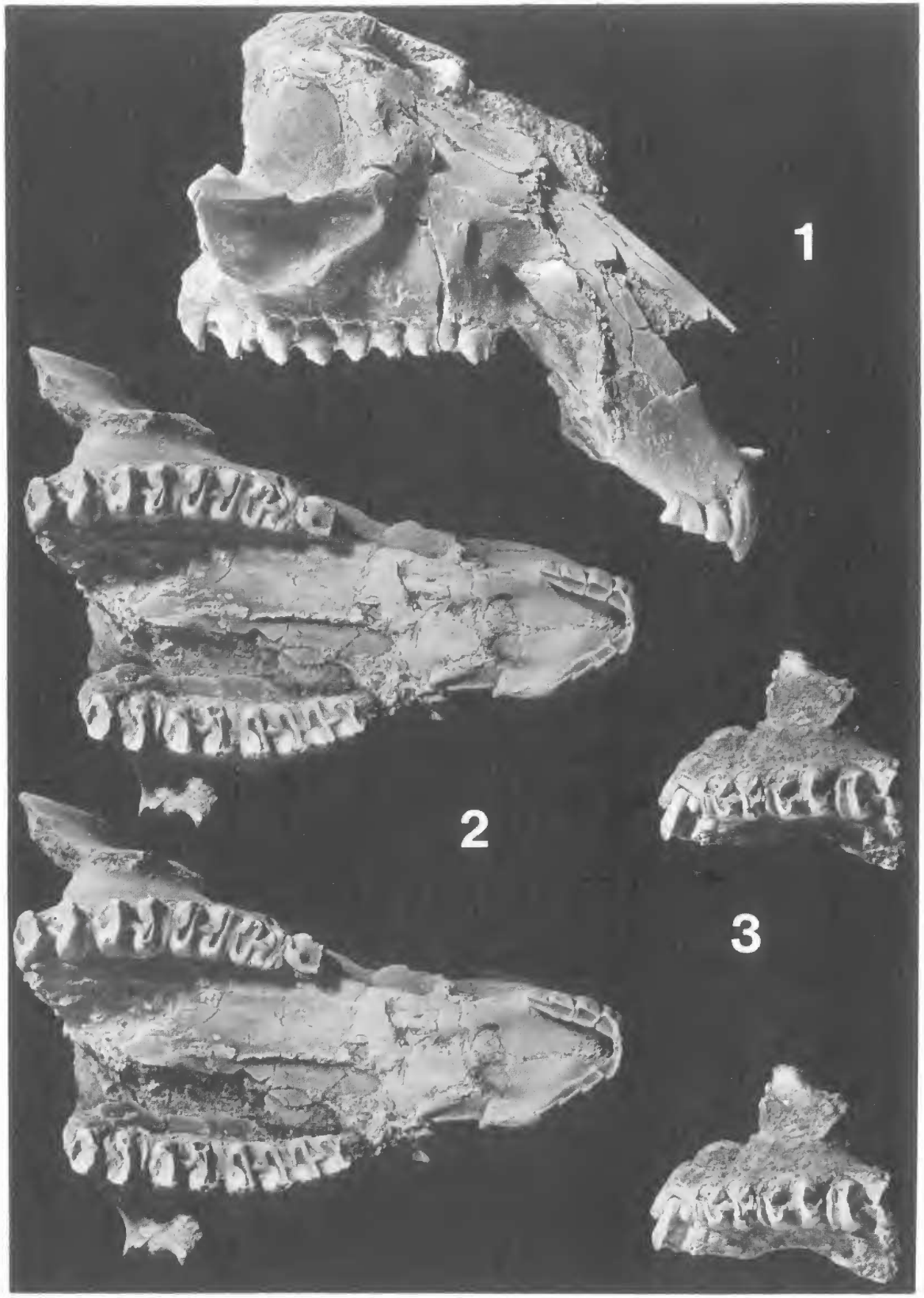

1
2
3

PLATE 23

FIG. 1: *Macropus (Prionotemnus) thor* (De Vis). Stereopair of occlusal view of adult partial left mandibular ramus, F4553, Clifton, Darling Downs, natural size.

FIG. 2: *Macropus (Prionotemnus) thor* (De Vis). Lateral view of F4553, natural size.

FIG. 3: *Macropus (?Prionotemnus) piltonensis* sp. nov. Stereopair of occlusal view of juvenile partial right mandibular ramus, F4576, Ravensthorpe, Pilton, Darling Downs, natural size.

FIG. 4: *Macropus (?Prionotemnus) piltonensis* sp. nov. Lateral view of F4576, natural size.

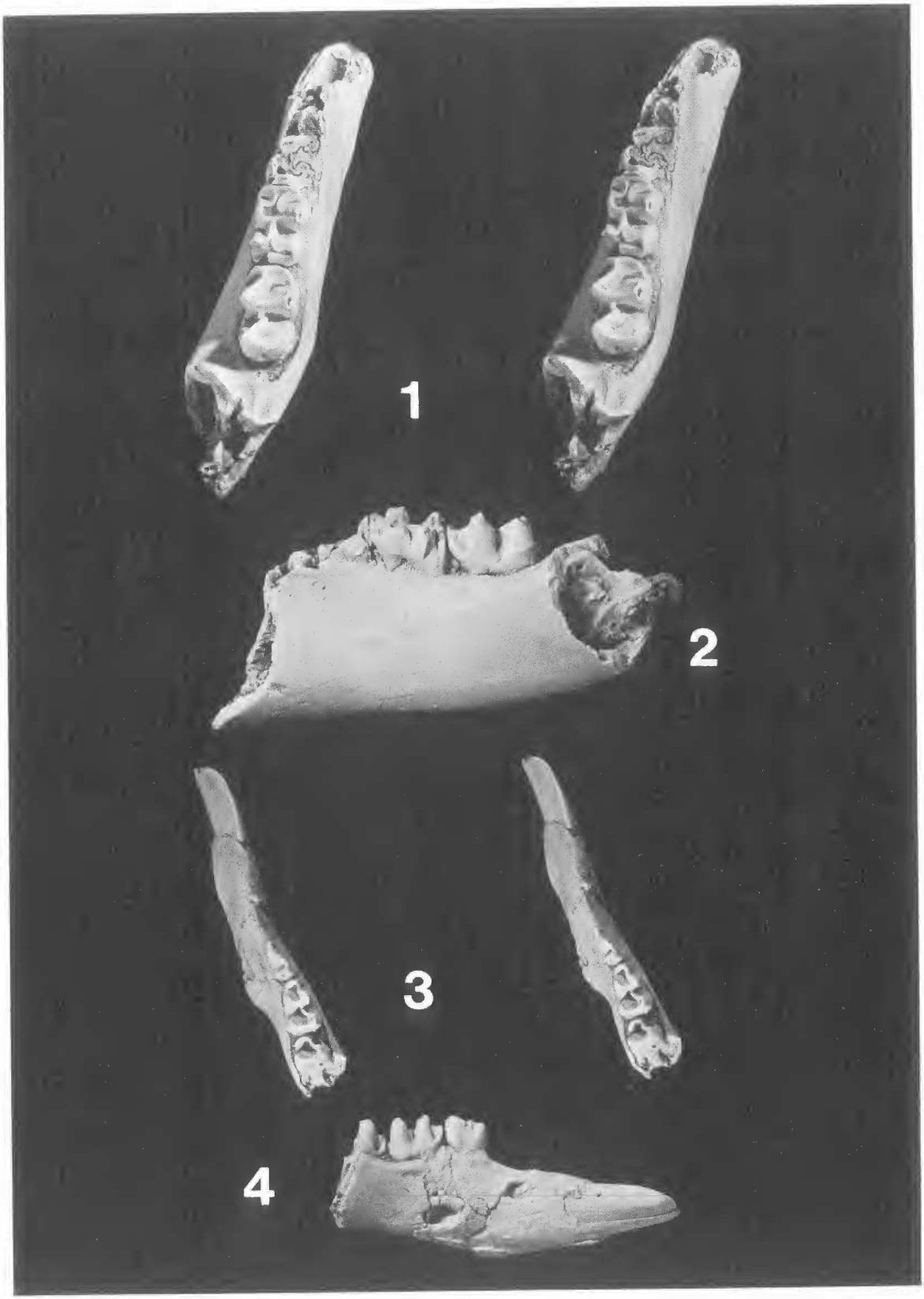

1
2
3
4

PLATE 24

FIG. 1: *Macropus (Prionotemnus) thor* (De Vis). Stereopair of palate of partial adult cranium, F4550, eastern Darling Downs, natural size.

FIG. 2: *Macropus (Prionotemnus) thor* (De Vis). Lateral view of partial cranium, F4550, natural size.

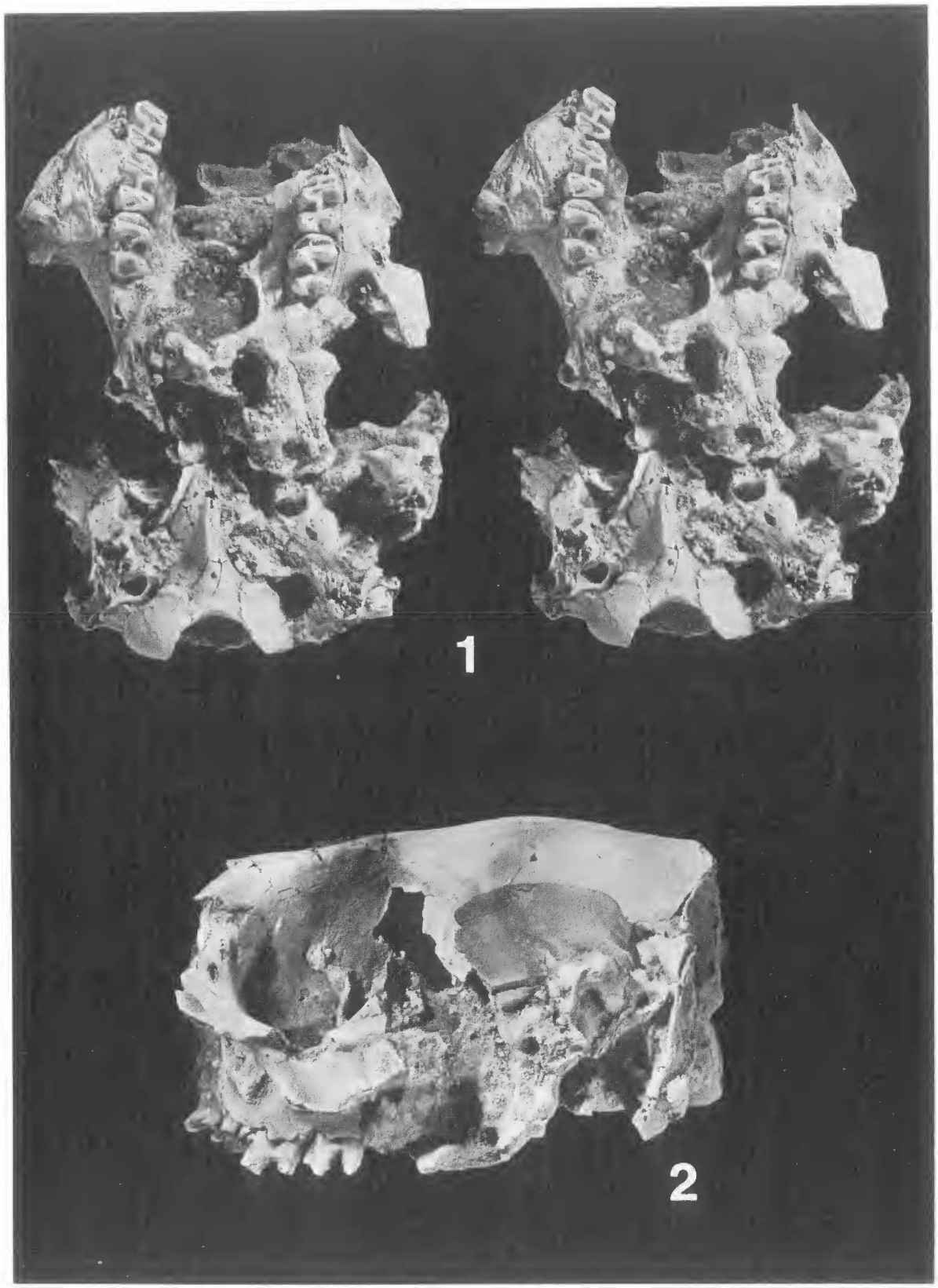

1
2

PLATE 25

FIG. 1: *Macropus (Prionotemnus) dryas* (De Vis). Lateral view of juvenile partial right mandibular ramus, F2508, Chinchilla, Darling downs, natural size.

FIG. 2: *Macropus (Prionotemnus) dryas* (De Vis). Stereopair of occlusal view of F2508, natural size.

FIG. 3: *Macropus (Prionotemnus) dryas* (De Vis). Lateral view of adult partial right mandibular ramus, F4590, Chinchilla, Darling Downs, natural size.

FIG. 4: *Macropus (Prionotemnus) dryas* (De Vis). Stereopair of occlusal view of F4590, natural size.

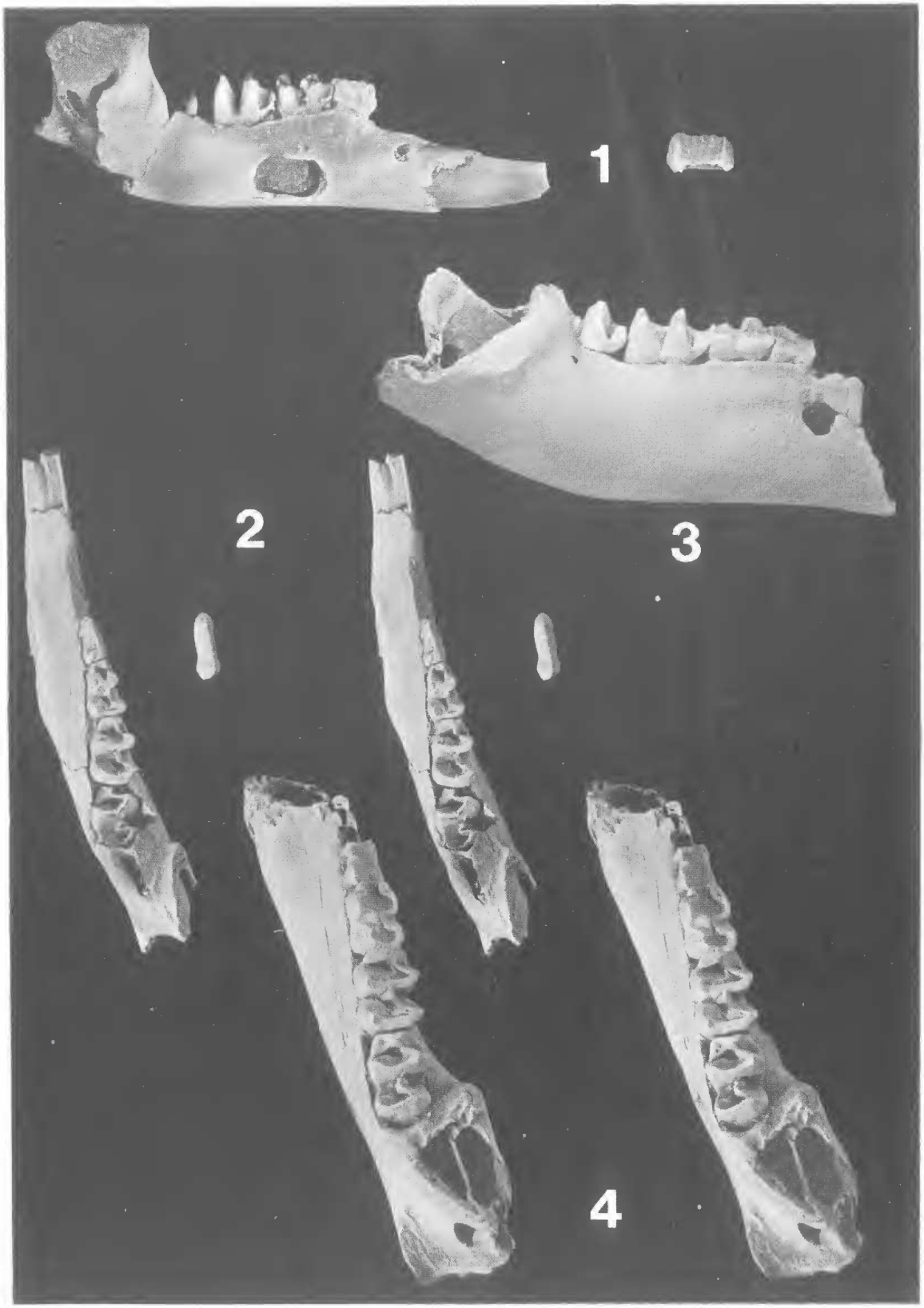

1
2
3
4

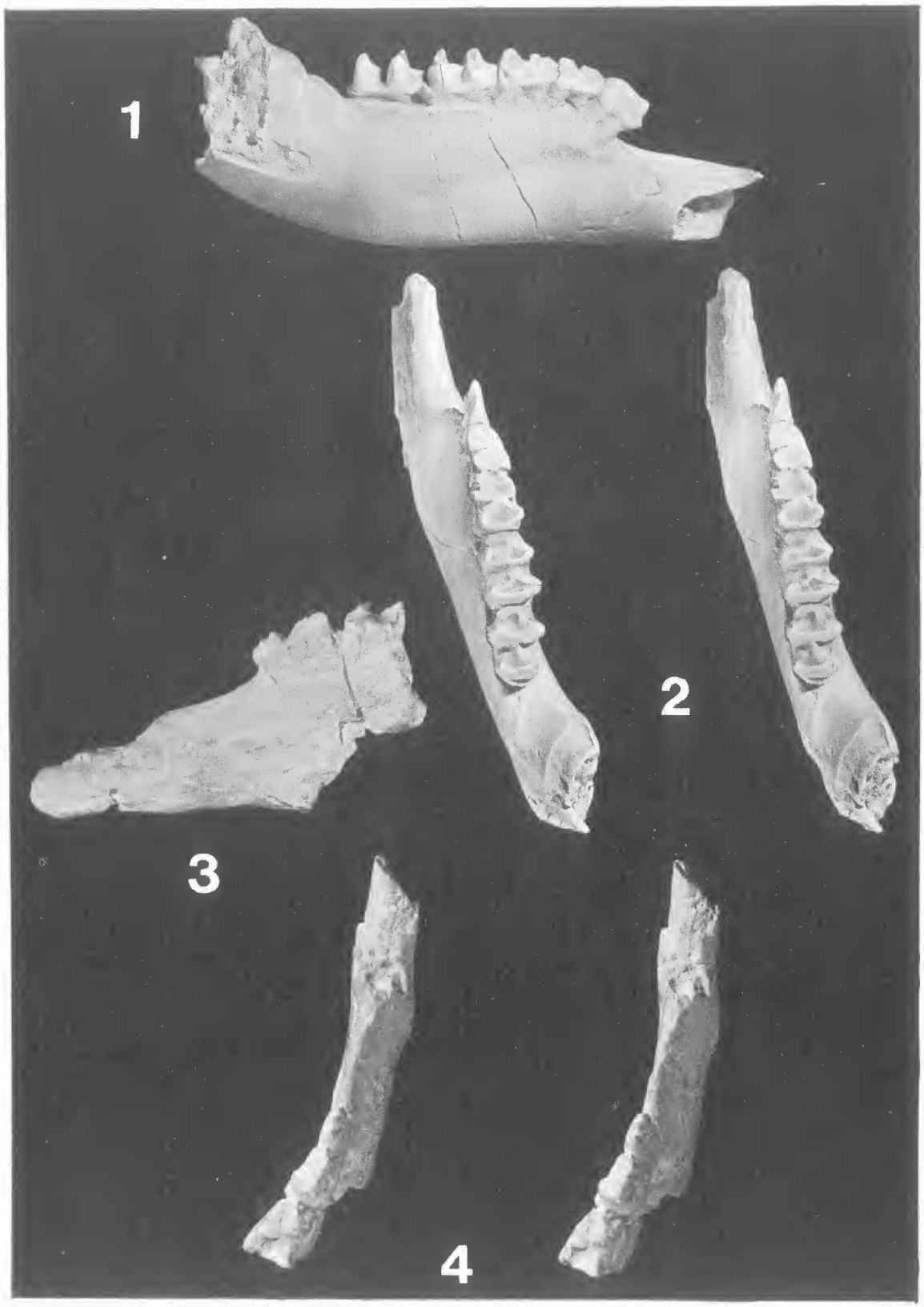
PLATE 26

FIG. 1: *Macropus (Prionotemnus) palankarinnicus* (Stirton). Lateral view of adult partial right mandibular ramus, F3589, western Darling Downs, natural size.

FIG. 2: *Macropus (Prionotemnus) palankarinnicus* (Stirton). Stereopair of occlusal view of F3589, natural size.

FIG. 3: *Macropus (Osphranter) altus* (Owen). Lateral view of cast of holotype of *Macropus cooperi*, F5608, Queensland, natural size.

FIG. 4: *Macropus (Osphranter) altus* (Owen). Stereopair of occlusal view of F5608, natural size.


1
2
3
4